National Library of Canada
Bibliothèque nationale du Canada

Canadian Theses Service
Service des thèses canadiennes

Ottawa, Canada
K1A 0N4

NOTICE

The quality of this microform is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

Reproduction in full or in part of this microform is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30.

AVIS

La qualité de cette microforme dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

Les documents qui font déjà l'objet d'un droit d'auteur (articles de revue, tests publiés, etc.) ne sont pas microfilmés.

La reproduction, même partielle, de cette microforme est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30.

NL-339 (r. 88/04)

Canada

THE UNIVERSITY OF ALBERTA

BEHAVIOURAL ADAPTIVE STRATEGIES OF WAPITI (*CERVUS ELAPHUS*) IN THE CANADIAN ROCKY MOUNTAINS

by

Luigi E. Morgantini

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY
IN
WILDLIFE PRODUCTIVITY AND MANAGEMENT

DEPARTMENT OF ANIMAL SCIENCE

EDMONTON, ALBERTA
FALL 1988

Permission has been granted to the National Library of Canada to microfilm this thesis and to lend or sell copies of the film.

The author (copyright owner) has reserved other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without his/her written permission.

L'autorisation a été accordée à la Bibliothèque nationale du Canada de microfilmer cette thèse et de prêter ou de vendre des exemplaires du film.

L'auteur (titulaire du droit d'auteur) se réserve les autres droits de publication; ni la thèse ni de longs extraits de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation écrite.

ISBN 0-315-45779-1

THE UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR LUIGI EMANUELE MORGANTINI

TITLE OF THESIS BEHAVIOURAL ADAPTIVE STRATEGIES OF WAPITI (_Cervus_ _elaphus_) IN THE CANADIAN ROCKY MOUNTAINS

DEGREE FOR WHICH THESIS WAS PRESENTED DOCTOR OF PHILOSOPHY

YEAR THIS DEGREE GRANTED FALL 1988

Permission is hereby granted to the UNIVERSITY OF ALBERTA LIBRARY to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly or scientific research purposes only.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

(SIGNED) ....

PERMANENT ADDRESS:

Site 3, Box 9, RR 2
Spruce Grove, Alta

DATED Oct 4, 1988

"The philosophical difficulty is the ease
with which ecological evidence
can be adduced to support theory,
when history has swallowed up
the circumstances of evolution."

J.S. Rowe 1983

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled BEHAVIOURAL ADAPTIVE STRATEGIES OF WAPITI (Cervus elaphus) IN THE CANADIAN ROCKY MOUNTAINS submitted by LUIGI EMANUELE MORGANTINI in partial fulfilment of the requirements for the degree of DOCTOR OF PHILOSOPHY in WILDLIFE PRODUCTIVITY AND MANAGEMENT.

A J Hudson

Supervisor

R J Christopherson

David R. Klein

External Examiner

Date October 4, 1988

For Raffaella

ABSTRACT

This study was designed to provide a better understanding of the ecology and behaviour of a wapiti population in the Canadian Rocky Mountains. The study centered on three major behavioural patterns; migrations, forage selection and habitat use.

Most of the animals wintered on three ranges outside Banff National Park, and migrated to summer alpine ranges in the Park, dispersing over 1,600 km^2 of mountainous terrain. The yearly migratory cycle ranged between 52 and 138 km with a minimum cumulative vertical movement of 2,000 m. The migratory pattern is interpreted as a vestige of the dispersal of wapiti from the point of reintroduction in the years 1917 and 1920. Habitual behaviour appeared to be a major factor in the use of seasonal ranges.

Diets consisted largely of grasses in winter (90%), spring (71%) and fall (72%). In summer, willows were the dominant dietary components (89%). The use of spring and summer ranges by wapiti coincided with a period of higher forage quality in those areas. Seasonal changes in diet composition and quality suggested that wapiti were attempting to maximize digestible energy intake in winter and nitrogen intake in summer.

Habitat selection reflected local vegetational structure, forage availability and quality, and security cover. Habitat

selection of males and females differed. The sexes were spatially separated and differenced in gregariousness. It was suggested that the evolution of sex segregation and differences in gregariousness may be related to reproductive behaviour.

Because behavioural patterns varied among individuals and herds, they should not be considered species-typical adaptations to the environment, but individual or population adjustments to local environments, i.e. behavioural adaptive strategies, expressions of the species ecological amplitude and versatility. Wapiti do not show fixed behavioural adaptations to any given environment. The adaptability of the species lies in its flexibility. This allows individuals to use different adaptive strategies under different environmental conditions.

ACKNOWLEDGEMENTS

I initiated this study in the fall of 1976. Intensive field work was completed in March 1980. However, through several other research projects in the area, I was able to study the wapiti population in the Red Deer-Panther-Clearwater River region to the present day. A study of this scope would not have been possible without the help and support of numerous individuals and Government Agencies.

I wish to thank my supervisor Dr. R.J. Hudson for his guidance, and for standing by me over all these years, hoping that one day I would finally write it all up. I would also like to thank the other members of my advisory committee, Dr. R. J. Christopherson and Dr. P. Woodard for patiently waiting and for their critical review of the study. My thanks are extended to Dr. P. J. Murphy and to Dr. B. R. Klein for their review of the manuscript and helpful, constructive criticisms.

Financial assistance during the first four years of study was obtained from the Alberta Fish and Wildlife Division which also provided transportation. I thankfully acknowledge Parks Canada Western Regional Office for providing radio-telemetry equipment.

I am especially grateful to the Warden Service of Banff National Park for its moral and logistic support, without which the study would not have been possible. Special thanks

are extended to P. Jacobson, D. Lowen, J. Wackerly, B. Browne, T. Skjonsberg, R. Kunelius, G. Antoniuk, E. Langshaw, and P. White for their interest in the study, for their help, and their willingness to share the joys and sorrows of their life in the wilderness. That friendship will be cherished for years to come.

I wish to thank the past and present staff of the Ya Ha Tinda Ranch (Slim Haugen, Earl Hays, the late Gordon Patterson, Cal Hays, Neil Plested) for their understanding and assistance.

The support, interest and friendship of Eldon Bruns, of the Alberta Fish and Wildlife Division in Rocky Mountain House, were a major asset of this study.

R. J. Klei and A. Kolenoski helped during the summers of 1977 and 1978.

Over the many years of this study, and of my graduate life, many individuals have helped with their expertise and/or moral support. To all of them, my heart felt thanks.

To my wife, Raffaella. No word can express my appreciation for the long and helpful discussions, for the encouragements, for her smile when I did not want to smile, for looking after the children and still able to continue her professional life, for her help which took numerous forms, too many to count.

And finally. Only the person who has spent many, many days riding through the mountains, following wapiti trails, can appreciate how valuable a good horse is. I would not have been able to complete the field study without the help of my horse, Bandit (Ban).

" To The Mountain Horse

His sire was Spain;
  His dam, the Nez-Perce
Legs forged on granite anvils;
  Heart forged by mountains.

Kin to the bighorn
  With clever hoof and infinite eye.
Drinker of the wind, the dawn-singer,
  Kin to the elk.

Enduring, gaunt, rock-worn,
  Lacking titled rank or registry,
His labors win the noble heights
  And the consort of eagles."

(John Madson. 1966.
The Elk. Winchester-Western Press.)

Thank you.

Table of contents

1. GENERAL INTRODUCTION..1

    1.1. Adaptations, adaptive strategies, and the environment..1

    1.2. Adaptations and adaptive behavioural strategies in wapiti..4

    1.4. Approach and thesis structure..6

    1.5. Literature cited..7

2. STUDY AREA AND ANIMAL POPULATION..10

    2.1. Vegetation and climate..10

    2.2. Animal population..14

    2.3. Literature cited..15

3. MIGRATORY PATTERNS..17

    3.1. Introduction..17

        3.1.1. The origin of migratory behaviour........17

        3.1.2. Migrations in wapiti..18

    3.2. Methods..21

    3.3. Results..22

        3.3.1. Winter distribution (Dec.-Apr.)........24

        3.3.2. Summer distribution (May-June)........28

        3.3.3. Spring and fall migrations........................29

        3.3.4. Intermediate ranges..32

3.3.5. Range fidelity..........................33
3.4. Discussion..................................35
3.4.1. Migrations in the study region........35
3.4.2. Original dispersal....................37
3.4.3. Migrations and the "familiar area" hypothesis............39
3.4.4. Adaptive significance of migratory patterns....................42
3.5. Conclusions.................................44
3.6. Literature cited............................44

4. FORAGE SELECTION..............................48
4.1. Introduction................................48
4.1.1. Diet composition......................48
4.1.2. Forage quality........................49
4.1.3. The nutritional significance of migrations........................49
4.2. Methods.....................................50
4.3. Results.....................................53
4.3.1. Diets.................................53
4.3.2. Forage quality........................53
4.3.3. Fecal indices.........................56
4.4. Discussion..................................58
4.4.1. Diet quality..........................58
4.4.2. Fecal nitrogen........................69

4.4.3. Adaptive significance of dietary changes....................70

4.5. Conclusions....................................72

4.6. Literature cited...............................73

5. HABITAT SELECTION 78

5.1. Introduction...................................78

5.1.1. Habitat selection and adaptation......78

5.1.2. Habitat selection in wapiti...........79

5.2. Methods..81

5.2.1. Habitat classification................81

5.2.2. Habitat selection......................81

5.3. Results..83

5.3.1. Habitat use 83

5.3.2. Herd size.............................90

5.3.3. Sex segregation.......................94

5.4. Discussion.....................................98

5.4.1. Habitat selection......................98

5.4.2. Sex differences in gregariousness....101

5.4.3. Sex segregation in habitat selection.105

5.4.3.1. Shank hypothesis...............106

5.4.3.2. Geist-Bromely hypothesis.......108

5.4.3.3. Geist-Petocz hypothesis........109

5.4.3.4. Morgantini-Hudson hypothesis...110

5.5. Conclusions...................................111

5.6. Literature cited..............................111

6. SYNTHESIS......................................116
    6.1. Overview...................................116
    6.2. Concluding remarks.........................120
    6.3. Literature cited...........................122

APPENDIX A. ANIMAL NUMBERS AND TRENDS.................124
1. POPULATION LEVELS..................................125
    1.1. Historical perspective.....................125
    1.2. From the 1950s to the present time.........128
        1.2.1. Banff National Park..................128
        1.2.2. Clearwater River (outside Banff National Park)..........129
        1.2.3. Red Deer and Panther Rivers (outside Banff national Park)........130
        1.2.4. Conclusions..........................139
2. PREDATION AND HUNTING LOSSES.......................140
    2.1. Predation..................................140
    2.2. Hunting and poaching.......................141
        2.2.1. Regulated hunting....................141
        2.2.2. Unregulated hunting..................143
3. POPULATION PRODUCTIVITY............................145
    3.1. Cow-calf ratios............................145
    3.2. Pregnancy rates............................149
    3.3. Population productivity model..............152

4. LITERATURE CITED..............................156

APPENDIX B. DISTRIBUTION, MOVEMENTS AND MIGRATIONS......161

1. Distribution and movements in winter (December-April)..............................162
    1.1. Red Deer River watershed....................162
    1.2. Clearwater River watershed..................166
    1.3. Panther River watershed.....................167
2. Distribution and movements in the summer.........168
3. Spring and fall migrations........................176
4. Herd boundaries...................................178
5. Literature cited..................................183

APPENDIX C...185

List of tables

Table Page

3.1. Summary of wapiti observations and estimated population sizes in the study region (1977-1979)....23

3.2. Distance between summer and winter ranges of 18 wapiti collared on the Ya Ha Tinda Ranch......27

3.3. Elevational distribution of wapiti before, during and after early snowfalls in 1977 and 1978..........31

3.4. Number of collared animals that returned to the same ranges in successive years (1977-1980).........34

4.1. Percent diet composition of wapiti on seasonal ranges in west-central Alberta based on fecal fragment analysis. January 1977-December 1978.......54

4.2. Percent crude protein content and IVDDM of composite range samples from seasonal ranges. January 1977-December 1978..........................55

4.3. Percent crude protein content and IVDDM of willow leaves and twigs from seasonal ranges. January 1977-December 1978..........................57

5.1. The 12 major habitats identified in the study area..82

5.2. Seasonal herd sizes in males and females wapiti in the Red Deer-Panther-Clearwater region. (1977-1979)......................................93

A.1. Winter surveys of wapiti in the Red Deer-Panther-Clearwater region..................................133

A.2. Wapiti surveys along the Red Deer and Panther River drainages, outside and inside Banff National Park. 1973-1977. Aerial survey data................135

A.3. Highest number of wapiti counted in the Red Deer-Panther-Clearwater region between 1983 and 1987, and estimated increment rates.....................138

A.4. Trophy wapiti harvest during the fall in Wildlife Management Units 416, 418, 420. (1975-1987)........142

A.5. Wapiti harvest during special winter hunting seasons on the Ya Ha Tinda Ranch (WMU 418) and the Corners (WMU 416) areas....................144

A.6. Calf/cow ratios of the wapiti population in the Red Deer-Panther-Clearwater region. 1977-1979......146

A.7. Pregnancy rates of female wapiti in late winter along the Red Deer and the Panther Rivers. 1969-1971 and 1973-1975.............................150

B.1. Location of summer ranges in Banff National Park and distances from the Ya Ha Tinda Ranch winter range (1977-1979)...........................177

C.1. Average size of cow-calf-yearling herds as determined by habitat. Winter.......................186

C.2. Average size of cow-calf-yearling herds as determined by habitat. Spring.......................187

C.3. Average size of cow-calf-yearling herds as determined by habitat. Summer.......................188

C.4. Average size of cow-calf-yearling herds as determined by habitat. Fall.........................189

C.5. Average size of bull herds as determined by habitat. Winter.......................190

C.6. Average size of bull herds as determined by habitat. Spring.......................191

C.7. Average size of bull herds as determined by habitat. Summer.......................192

C.8. Average size of bull herds as determined by habitat. Fall.........................193

List of figures

Figure page

2.1. Study area....................................12

3.1. Migratory patterns of wapiti in the Red Deer-Panther-Clearwater region (1977-1980)...............26

3.2. Original dispersal of wapiti in the Red Deer-Panther-Clearwater region, as proposed by this study........41

4.1. Crude protein in forage and feces from different seasonal ranges in the Red Deer-Panther-Clearwater region along the east slopes of the Rocky Mountains (1977-1978)......................................60

4.2. Relationship between fecal nitrogen and estimated nitrogen content of diet of wapiti in the Red Deer-Panther-Clearwater region along the east slopes of the Rocky Mountains (1977-1978)...........62

4.3. Relationship between fecal lignin and browse content of diet of wapiti in the Red Deer-Panther-Clearwater region along the eastern slopes of the Rocky Mountains (1977-1978)...........64

4.4. Fecal lignin, fecal ash, and browse dietary component of wapiti in the Red Deer-Panther-Clearwater region along the east slopes of the Rocky Mountains (1977-1978)...........66

5.1. Seasonal habitat selection of wapiti (all sexes) based on the distribution of group observations in the Red Deer-Panther-Clearwater region along the east slopes of the Rocky Mountains (1977-1978)......86

5.2. Habitat selection of wapiti (all sexes) in the Red Deer-Panther-Clearwater region along the east slopes of the Rocky Mountains. A comparison between seasonal habitat selection based on the distribution of group observations and habitat selection based on the total number of animals counted (1977-1979)..................................89

5.3. Sizes of male and female wapiti herds in the Red Deer-Panther-Clearwater region along the east slopes of the Rocky Mountains (1977-1978)...........92

5.4. Seasonal habitat selection (individual observations) between bulls and cow-calf-yearling in the Red Deer-Panther-Clearwater region along the east slopes of the Rocky Mountains........................96

A.1. Population model of two wapiti female herds under three different levels of mortality.................155

B.1. Map of study region....................................164

B.2. Summer (July-August) distribution of wapiti sightings...170

B.3. Summer (July-August) distribution of collared wapiti..173

B.4. Late spring movements of 9 collared wapiti from winter to summer ranges (1978)................180

B.5. Fall movements of 7 collared wapiti from summer to winter ranges..................................182

1. GENERAL INTRODUCTION

1.1. Adaptations, adaptive strategies, and the environment

Species evolution is the process of adaptation to new facets of the environment. Whether the adaptation is related to new altered features of the environment, or to expansion into previously unavailable niches, it is generally agreed that it is the variety of population-environment interactions that allows for different patterns of evolution (Dobzhansky *et al*. 1977). In this context, the term environment describes all physical, chemical, biological and behavioural factors surrounding the individual, including other individuals of the same or different species.

"Evolutionary adaptation in its strict sense refers to hereditary adjustment ... between the whole (living) system and its environment" (Allee *et al*. 1949:630). Thus, an adaptation is something new, arisen through the process of natural selection in response to altered environmental demands. On the other hand, pre-adaptations are physical or behavioural characteristics that are present before an environmental change, and that 'accidentally' become valuable for the survival of the species (Mayr 1974).

Various authors have proposed different criteria to identify an adaptation. Ayala (1968,1970) suggested that useful functionality of a characteristic is an acceptable criterion, if that usefulness can be directly related to the development of the feature. A contrasting view is presented by Williams (1966:212), who stated: "...the demonstration of effects, good or bad, proves nothing. To prove adaptability one must demonstrate a functional design." But no functionality can be completely understood if the environmental context that shaped it is not examined in detail.

Adaptations spread through the species at the speed of reproduction and natural selection. Although selective pressures could be heightened during times of large and widespread environmental changes (Geist 1987), most macroscopic environmental modifications occur on a geological time scale. Long intervals of relatively stable macro-environmental conditions allow for adaptations to become established throughout the species. Fast and successful colonization of newly opened niches can be accomplished through pre-adapted traits (Mayr 1974).

On a micro-scale, environmental changes happen more quickly and unpredictably. Day-to-day variations in temperature, precipitation, and weather conditions, food quality and availability, seasonal and life cycles, all present each individual with a wide range of different environmental conditions. To cope with micro-environmental changes, adaptive strategies come into play. As opposed to the more rigid constraints of adaptations, evolved within the more predictable limits of the macro-environment, adaptive strategies allow individuals a wide variety of different responses to current environmental conditions.

The concept of adaptive strategies was used by Levins (1968:10) to describe adaptations not to a particular environment, but "...to the pattern of the environment in space and time, to temporal variability, (and) to environmental uncertainty". In his paper on behavioural adaptive strategies of wapiti, Geist (1982:220) defines adaptive strategies as "...behavioural patterns and bodily features organized so as to enable the individual to adjust best to its environment". However, Geist's use of the term "adaptive strategy" appears different from Levins' in that it often refers to species-specific characteristics evolved to fit the species into a particular niche. For instance, under the umbrella definition of adaptive strategies, Geist includes such physiological characteristics as "dealing with parasites and pathogens, ...and wound healing" (p. 220), and such behaviours as courtship (p. 258), which are well established in their patterns throughout the species.

For the purpose of clarity, and to help better distinguish between adaptations and adaptive strategies in wapiti, the term "adaptation" will be used in this study to indicate species-specific responses to the macro-environment, while the term "adaptive strategy" will denote group or individual responses to the micro-environment.

1.2. Adaptations and adaptive behavioural strategies in wapiti

In general, ungulates are thought to have adapted to poor forage quality by increasing intake and/or retention time through physiological and morphological adaptations of their digestive tract (Hoffman 1973; Van Soest 1982). These adaptations have occurred within the constraints of body size, that in turn may have been shaped by climate (Kleiber 1975, Gordon 1972), predation (Geist 1974), forage quality and availability (Bell 1969, 1971; Jarman 1974, Case 1979, Renecker 1987), and reproductive behaviour demands (Geist 1987).

Wapiti, living in northern environments, endure long, harsh winter conditions, frequently feeding on forage which fails to meet minimum maintenance requirements (Gates 1980, Nelson and Leege 1982, Morgantini and Hudson 1985). In spring and summer, high quality forage is critical to restore body tissue and to meet the additional energy demands of calving and lactation (Moen 1973). At this time, weight gain is essential to ensure that adequate energy stores are available to subsidize a meager winter diet. Under these conditions, the presence of behavioural patterns and physiological mechanisms which maximize forage quality and intake in the summer, while minimizing energy expenditures, appears to be beneficial to the species. Hence, migrations (Craighead et al. 1973), shifts in feeding habits (Nelson and Leege 1982), and habitat preferences (Skovlin 1982) could be seen as adaptations that allow the species to adjust to seasonal environments. However, if behavioural patterns vary among individuals, herds and populations, they should not be considered species-specific behavioural adaptations to the environment, but individual or population adjustments to local environments, i.e. behavioural adaptive strategies [Chapter 1.1], expressions of the species ecological amplitude and versatility.

Further, the fact that behavioural patterns beneficial to wapiti exist today does not per se mean that these patterns evolved as species response to today's environment. As properly stated by Williams (1966:29):

> "...the mere presence of an adaptation is no argument for its necessity, either for the individual or the population. It is evidence only that during the evolutionary development of the adaptation the genes that augmented its development survived at a greater rate than those that did not... ecological or physiological necessity is not an evolutionary factor".

Present behavioural patterns of the species may be only genetic by-products, or they may represent pre-adaptations, evolved under the influence of earlier and different selective forces.

1.3 Approach and thesis structure

Recently, an attempt has been made to develop an all-encompassing theory that, based on the recent evolutionary history of wapiti in periglacial regions, attributes adaptive value to the species ecological and behavioural patterns (Geist 1982). However, in this theory little acknowledgement is made of the complexity of individual-environment interactions, and of the numerous interrelations between morphology, physiology, nutrition, ecology and social behaviour that can be found (Geist 1974, 1978; Leuthold 1977, Hudson 1985). Analysis of the adaptive significance of any one morphology or behaviour can be very misleading, since cause-effect relationship may not be substantiated (Leuthold 1977). Further, the theory, in its present form, tends to confuse species-specific "adaptations" with individual adaptive strategies. For these reasons, it seems that the development of an all-encompassing theory to explain wapiti ecological and behavioural patterns, though logically elegant, does not help in understanding this species. On the contrary, because of unavoidable wide-sweeping generalizations, it may obscure ecological, behavioural, or local environmental factors.

This study was designed to provide a better understanding of the ecology and behaviour of a wapiti population along the eastern slopes of the Canadian Rocky Mountains. In this region, I sought to describe and analyze three major behavioural patterns and to assess their adaptive value for the species. The hypothesis was the following:

> Behavioural patterns (migratory behaviour, forage and habitat selection) of wapiti in the region represent adaptations to the northern environment, instead of individual or group responses to local environmental conditions (adaptive strategies).

The study consisted of three different components, the respective objectives of which were:

1. To determine the existence and extent of migratory patterns and their adaptive significance [Chapter 3].
2. To assess the nutritional significance of seasonal changes in food habits and forage quality [Chapter 4].
3. To describe patterns of habitat selection and use in mountain environments, in terms of their evolutionary significance [Chapter 5].

The concepts developed in chapters 3, 4 and 5 are summarized and integrated in a concluding synthesis.

1.4 Literature cited

ALLEE, W. C., A. E. EMERSON, O. PARK, T. PARK and K. P. SCHMIDT. 1949. Principles of animal ecology. W.B. Saunders Company. Philadelphia and London. 837pp.

AYALA, F. J. 1968. Biology as an autonomous science. Am. Sci. 56:207-221.

AYALA, F. J. 1970. Teleological explanations in evolutionary biology. Philos. Sci. 37:1-15.

BELL, R. H. V. 1969. The use of the herb layer by grazing ungulates in the Serengety. Pages 111-123 in A. Watson (Ed.), Animal populations in relation to their food resources, Symp. Brit. Ecol. Soc., Blackwell Sci. Pub., Oxford.

BELL, R. H. V. 1971. A grazing system in the Serengeti. Sci. Am. 225: 86-93.

CASE, T. J. 1979. Optimal body size and an animal's diet. Acta Biotheoretica 28: 54-69.

CRAIGHEAD, J. J., G. ATWELL, and B. W. O'GARA. 1972. Elk migrations in and near Yellowstone National Park. Wildl. Monogr. No.29. 49pp.

CRAIGHEAD, J. J., F. C. CRAIGHEAD Jr., R. L. RUFF, and B. W. O'GARA. 1973. Home ranges and activity patterns of non-migratory elk of the Madison drainage herd as determined by byotelemetry. Wildl. Monogr. No.33. 50pp.

DOBZHANSKY, T., F. J. AYALA, G. L. STEBBINGS and J. W. VALENTINE. 1977. Evolution. W. H. Freeman and Co., San Francisco. 572pp.

GATES, C. C. 1980. Patterns of behaviour and performance of wapiti (Cervus elaphus nelsoni) in the boreal mixed wood forest. Ph.D. Thesis, Univ. Alberta, Edmonton. 240pp.

GEIST, V. 1974. On the relationship of social evolution and ecology in ungulates. Amer. Zool. 14: 205-220.

GEIST, V. 1978. Life strategies, human evolution, environmental design. Towards a biological theory health. Springer-Verlag, New York. 495 pp.

GEIST, V. 1982. Adaptive behavioral strategies. Pages 219-278 in J. W. Thomas and D. E. Toweill (Eds.), Elk of North America. Ecology and management. Stackpole Books, Harrisburg, Pa.

GEIST, V. 1987. On the speciation of Ice Age mammals, with special reference to cervids and caprids. Can. J. Zool. 65: 1067-1084.

GORDON, M. S. 1972. Animal physiology: principles and adaptations. The Macmillan Co., New York. 592pp.

HOFFMAN, R. R. 1973. The Ruminant Stomach. E. Afr. Monogr. in Biol., 2. East African Literature Bureau, Nairobi. 354pp.

HUDSON, R. J. 1985. Body size, energetics and adaptive radiation. Pages 1-21 in R. J. Hudson and R. G. White (Eds.), Bioenergetics of wild herbivores. CRC Press, Boca Raton, Florida.

JARMAN, P.J. 1974. The social organization of antelope in relation to their ecology. Behavior 48: 215-266.

KLEIBER, M. 1975. The fire of life. R. E. Kreiger Co., Huntington, New York. 453pp.

LEUTHOLD, W. 1977. African ungulates. Springer-Verlag, New York. 307pp.

LEVINS, R. 1968. Evolution in changing environments. Princeton Univ. Press, Princeton. 120pp.

MAYR, E. 1974. Populations, species and evolution. Belknap Press. Harvard University Press. Cambridge, Massachusetts. 453pp.

MOEN, A. N. 1973. Wildlife ecology: An analytical approach. W. H. Freeman and Co., San Francisco, Calif. 458pp.

MORGANTINI, L. E. AND R. J. HUDSON. 1985. Changes in diets of wapiti during a hunting season. J. Range Manage. 38: 77-79

NELSON, J. R. AND T. A. LEEGE. 1982. Nutritional requirements and food habits. Pages 323-368 in J. W. Thomas and D. E. Toweill (Eds.), Elk of North America. Ecology and management. Stackpole Books, Harrisburg, Pa.

RENECKER, L. A. 1987. Bioenergetics and behaviour of moose (Alces alces) in the aspen boreal forest. Ph.D. Thesis. Univ. Alberta, Edmonton.

SKOVLIN, J. M. 1982. Habitat requirements and evaluations. Pages 369-414 in J. W. Thomas and D. E. Toweill (Eds.), Elk of North America. Ecology and management. Stackpole Books, Harrisburg, Pa.

VAN SOEST, P. J. 1982. Nutritional ecology of the ruminant. O & B Books Inc., Corvallis, Or. 374pp.

WILLIAMS, G. C. 1966. Adaptation and natural selection. Princeton University Press, Princeton, N. J. 307pp.

2. STUDY AREA AND ANIMAL POPULATION

The study was conducted in the Canadian Rocky Mountains, in west-central Alberta (Figure 2.1). The study area extends over 4000 km^2 of mountain terrain, of which 80% is within the boundary of Banff National Park. It includes four major river valleys: the Red deer, Clearwater, Panther and Pipestone Rivers. Elevation ranges between 1500 m on valley floors and 2600 m on alpine sites. Detailed description of the study area is found in Holland and Coen (1982) for Banff National Park, and in Morgantini (1979) and Morgantini and Russel (1983) for the area outside the National Park.

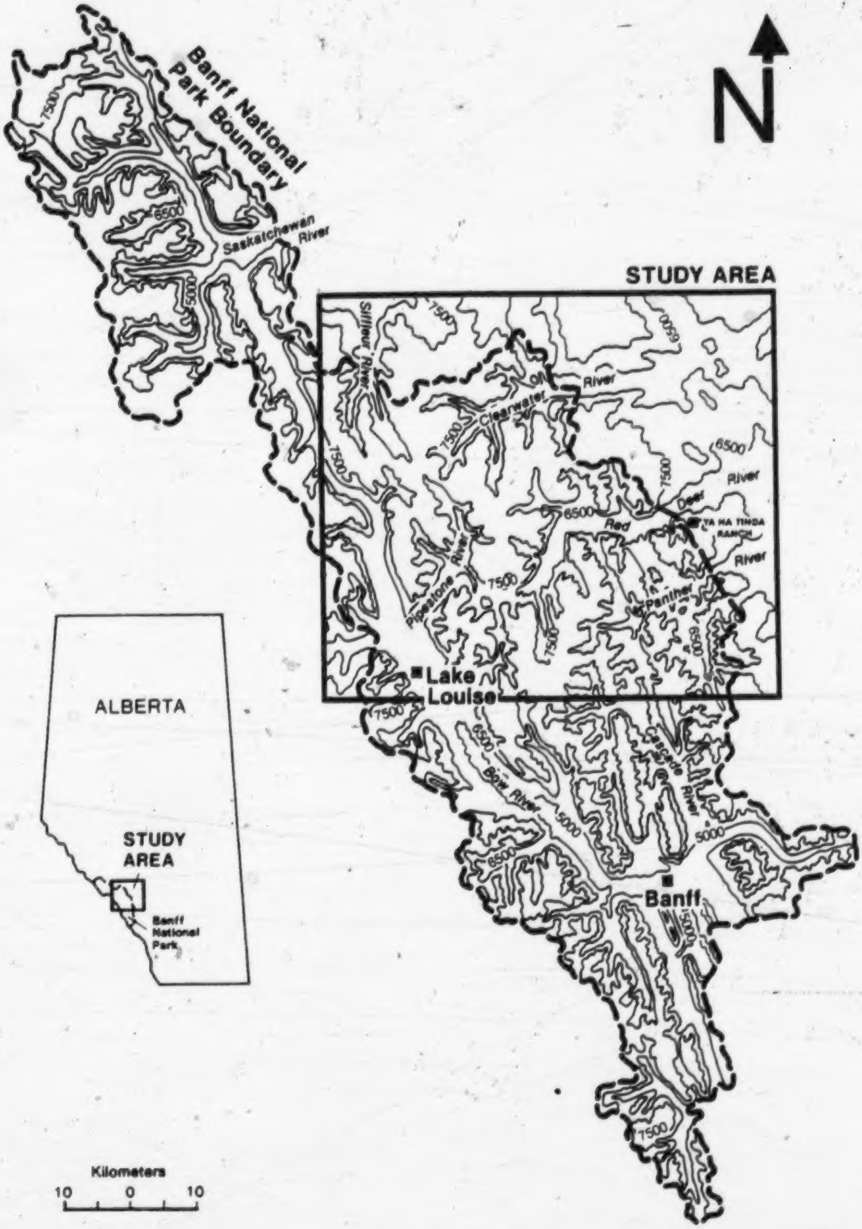
2.1. Vegetation and climate

Three ecoregions are identified (Stelfox 1981, Holland and Coen 1982). The Alpine Ecoregion occurs at elevations above 2300 m, and is characterized by cold harsh climatic conditions and the absence of trees. Plant communities are those typical of alpine heath tundra. Graminoids, sedges and forbs are common within a dominant mat of low growing willows (_Salix_ _arctica_ and _Salix_ _nivalis_)[1]. Depending on winter severity, this Ecoregion is snow covered from late October

---

[1] Moss, E.H. 1974. Flora of Alberta. Univ. of Toronto Press. 546pp. was used as the source for botanical nomenclature.

FIGURE 2.1. The Red Deer-Panther-Clearwater river study area


N
Banff National Park Boundary
Saskatchewan River
STUDY AREA
Siffleur River
Clearwater River
Red Deer River
YA HA TINDA RANCH
River
Panther
Pipestone River
Lake Louise
Bow River
Cascade River
Banff
7500
6500
5000
ALBERTA
STUDY AREA
Banff National Park
Kilometers
10
0
10

Base map adapted from Holroyd and Van Tighem, 1983.

until May. The growing season is restricted to less than 60 days.

The Subalpine Ecoregion ranges between 1600 m and 2300 m and extends over most of the study area. Forests are dominated by Engelman spruce (*Picea engelmanii*) and subalpine fir (*Abies lasiocarpa*). White spruce (*Picea glauca*) and lodgepole pine (*Pinus contorta*) are found at lower elevations. Shrub and grass meadows occur along river and stream drainages, and on alluvial flats. Dry grasslands and shrublands are present in the eastern section of the Ecoregion. Willow species (*Salix* spp.) and dwarf birch (*Betula glandulosa*) are the dominant shrubs. Wildrye (*Elymus innovatus*), wheatgrass (*Agropyron* spp.), june grass (*Koeleria cristata*), bluegrass (*Poa* spp.), and oatgrass (*Helictotrichon hookerii*) are the most common grass species.

The climate of the Subalpine Ecoregion varies depending on site-specific topography and elevation. The mean yearly temperature at low elevations is about 0° C (Holland and Coen 1982). Snow cover tends to persist through the winter. However, in the eastern section of the study area (Red Deer, Panther, Clearwater region) winter precipitation is lower than in the western section (Pipestone, Lake Louise region). In the Red Deer, Panther and Clearwater region strong westerly winds maintain grass meadows along the main river valleys snow free, generating extensive snowdrifts that persist throughout

A

the winter.

The Montane Ecoregion is restricted to alluvial meadows along the main river valleys outside Banff National Park (Stelfox 1981). Three areas can be identified: the Ya Ha Tinda Ranch along the Red Deer River, the Corners along the Panther River, and Harrison Flats along the Clearwater River. Due to the sheltering effect of the surrounding mountains (rain shadow effect), these meadows have mild winters. Strong westerly flow and low precipitation combine to maintain native fescue grassland (Looman 1969) snowfree over most of the winter. The vegetational mosaic is characterized by rolling rough fescue (*Festuca scabrella*) grasslands surrounded by aspen (*Populus tremuloides*) and lodgepole pine forests. Douglas fir, a species characteristic of Montane ecoregions, is not present possibly due to the relative isolation of the areas (Stelfox 1981). Willow species and dwarf birch are abundant in the transition zone between open grassland and forest. Detailed classification of plant communities is found in Morgantini and Russell (1983).

2.2. Animal population

The study area supports one of the most important wapiti populations in the province of Alberta. At the time of the study, it consisted of some 1000 animals of which an estimated 600 were found in the Pipestone-Red Deer River region. The

Panther and Clearwater region supported about 200 individuals each.

When this study was initiated, very little was known about the distribution and ecology of the wapiti population. The only data available were based on occasional winter aerial surveys conducted by the Alberta Fish and Wildlife Division or on incidental observations by Banff National Park wardens, locals and old-timers.

During this study, a major effort was made to gain a better understanding of the wapiti population in the region. A summary of historical and present animal numbers, population trends and productivity is presented in Appendix A. This summary is based on data collected during this study, on incidental observations collected to date, and on an extensive search and analysis of published and unpublished reports.

2.3. Literature cited

HOLLAND, W. D., and G. M. COEN. 1982. Ecological (biophysical) land classification of Banff and Jasper National Park. Vol. II: Soil and Vegetation Resources. Alberta Institute of Pedology Publ. No. SS-82-44.

LOOMAN, J. 1969. The fescue grasslands of western Canada. Vegetatio 19: 128-145.

MORGANTINI, L. E. 1979. Habitat selection and resource division among bighorn sheep, elk and mule deer in western Alberta. M.Sc. Thesis, Univ. Alberta, Edmonton. 187pp.

MORGANTINI, L. E., and W. B. RUSSELL. 1983. An assessment of three selected elk winter ranges in the Rocky

Mountains Region. Unpubl. Rep. prepared for the Alberta Fish and Wildlife Division by Wildlife Resources Consulting Ltd. Edmonton. Alberta Fish and Wildlife Files, Edmonton. 265pp.

STELFOX, H. A. 1981. Ecological land classification: Red Deer-James River. Alberta Energy and Natural Resources. Resource Evaluation and Planning Division. Report No. T/11-No.8. 112pp.

3. MIGRATORY PATTERNS*

3.1. Introduction

3.1.1. The origin of migratory behaviour

Since Aristotle first noted that birds migrate, several theories have been developed on the origin and evolution of migratory behaviour (Cox 1966, Baker 1978). Although most of them are based on observations of the ecology and behaviour of bird populations, attempts have been made to develop a general evolutionary theory applicable to mammals, fish and invertebrates.

Cox (1966) hypothesized that intraspecific and interspecific competition may be the primary selective agent in the evolution of migrations in resident populations. Increased use of seasonably favourable adjacent areas would allow greater survival and/or reproduction rates. Cohen (1967) indicated that regular seasonal migrations are an adaptation to periodically unfavorable environmental conditions. Baker (1978, 1982), in an extensive and comprehensive review, suggested that migratory behaviour consists of three major features: initial exploratory behaviour, habitat ranking, and development of familiar areas.

---

* A version of this chapter has been accepted for publication. Morgantini, L.E. and R.J. Hudson. 1988. Can. Field Nat. (in press)

Exploratory behaviour is distinguished from dispersal as it involves a return to the point of origin. Its evolution may have been dictated by a continuing search for habitats and resources that can maximize reproductive fitness. During exploratory movements animals encounter numerous habitats. Their optimum behaviour is to rank them in order of suitability and to develop "familiar areas" (Baker 1978). Seasonal return migrations, in response to environmental cues, involve the return to seasonally suitable habitats that had been previously experienced and of which animals retain spatial memory.

3.1.2. Migrations in wapiti

In mountainous regions, most wapiti populations migrate among seasonal ranges (Altmann 1952, Craighead *et al*. 1972). Migratory behaviour may vary from local movements of 2-4 km (Anderson 1958, Dalke *et al*. 1965) to migrations of more than 100 km (Skinner 1925, Anderson 1958). Within the same population, migratory and non migratory behaviour may be present (Martinka 1969, Boyd 1970). Some herds exhibit spring and summer migrations, whereas others remain on winter ranges until early summer (Knight 1970).

Within the diversity of migratory patterns, wapiti show considerable fidelity to seasonal ranges year after year (Murie 1951, Altmann 1952, Anderson 1958, Knight 1970). In the Yellowstone National Park area, although some mingling occurs on summer ranges, most animals return to different winter ranges, thus maintaining distinct herds (Craighead _et al_. 1972). The same migratory routes may be used every year (Altmann 1952, Anderson 1958).

While migratory behaviour of wapiti in the United States has been well documented, knowledge of migrations in the Canadian Rocky Mountains is limited to observations of seasonal range use and animal distribution, obtained incidentally during studies of herbivore interactions, population dynamics or wolf predation (Cowan 1950, Flook 1970, Stelfox 1974, Carbyn 1974).

The factors governing migratory behaviour are little understood. Casual observations, based largely on the use of winter ranges in relation to weather conditions, suggest that wapiti move to areas providing the best foraging opportunities (Skinner 1925, Murie 1951, Ward _et al_. 1973). Other studies have indicated that factors such as spring calving (Brazda 1953) and insect harassment (Darling 1937) may be more important. Fall movements to winter ranges have been related to snow accumulation at higher elevations (Murie 1951, Leege and Hickey 1977).

Geist (1982) suggested that wapiti, as a highly opportunistic species, should be expected to follow plant growth along an elevational gradient so as to maximize energy intake and reproductive fitness. Geist's hypothesis implies that migratory behaviour evolved as a species-specific adaptation to seasonal environments. However, the variety of migratory and non-migratory patterns within and between different wapiti populations (Martinka 1969), indicates that migratory behaviour is not an essential trait for reproductive success. Present day migratory behaviour might be a pre-adaptation, that is, a behavioural pattern which originally developed as an exploratory-dispersal mechanism and that was maintained since it did not interfere with the species' reproductive fitness. Today's apparent advantages (better nutrition, insect avoidance, etc.) of migrating onto high elevation ranges may confer fortuitous benefits to individuals that have learned to avoid their winter ranges during the summer. Tradition (Wynne-Edwards 1962) may be a major factor in maintaining the migratory trait, shaping the existence and patterns of migrations in wapiti (Murie 1951).

This chapter delineates wapiti distribution and movements in the Panther, Red Deer and Clearwater River region and relates present migratory patterns to the dispersal of wapiti from Banff National Park after their reintroduction in the Bow River valley in 1917 and 1920. Specifically, this chapter intends to provide a better understanding of migratory patterns of wapiti in the study area, as a part of the wider objective of assessing their adaptive value.

3.2. Methods

Data were collected through three complementary sources: ground surveys, aerial surveys and radio-telemetry.

Most of the data were collected during extensive field surveys carried out on foot or on horse-back throughout the study area. The study period extended from December 1976 to November 1979. Every month an average of 15 days were spent in the field, for a total of 537 field-days. Field work consisted of locating wapiti herds and continuously monitoring their daily movements throughout the field period. Animal movements and distributions were photo-documented in the field and later reported on 1:21000 scale aerial photographs.

Occasional surveys were also conducted between 1980 and 1987, but were only used to confirm the stability of regional movements and distributions.

The identification of herds and the location of seasonal ranges was initially facilitated by the presence of 11 cows (6-year old and older) equipped with neck collars. These animals had been collared in 1971 and 1973 by the Alberta Fish and Wildlife Division as part of an uncompleted study on Wapiti movements in the Ya Ha Tinda Ranch area along the Red Deer River. However, in order to further facilitate the identification of different herds and to follow the animals during their long seasonal movements, an additional four cows (5-year old and older), four yearlings (two males and two females) and three calves (one male and two females) were trapped and radio-collared.

During the summers of 1977 and 1978, 7 aerial surveys (27.4 hours) were carried out with a Bell 206 Helicopter. The study area was surveyed by flying all the major and secondary valleys in a pattern to allow maximum coverage of alpine-subalpine ranges and of meadows and forests in the region. In the winters of 1976-77, 1977-78, and 1978-79, similar aerial surveys were conducted by the Banff National Park Warden Service and by the Alberta Fish and Wildlife Division inside and outside the National Park, respectively (Banff National Park Files; Alberta Fish and Wildlife Files).

3.3. Results

During the three year study, 652 group observations were made (Table 3.1). A cumulative total of 14,758 animals were counted. Collared animals were present in 199 group observations for a total of 248 sightings.

Most observations were recorded in the Red Deer River watershed which supported an estimated population of 600 animals. Wapiti along the Little Pipestone and the Pipestone Rivers were also found to be part of the Red Deer River herd. The Clearwater and the Panther River supported about 200 individuals each.

The entire yearly migratory cycle of the wapiti

Table 3.1. Summary of wapiti observations and estimated population sizes in the study region (1977-1979).

River Drainage	Estimated Pop. Size	No. of observations Winter (Dec-Apr)	 Spring (May-June)	 Summer (July-Aug)	 Fall (Sept-Nov)
Red Deer*	600	175 (8144)	122 (154)	80 (994)	57 (751)
Clearwater	200	47 (343)	31 (613)	13 (122)	11 (149)
Panther	200	38 (916)	24 (387)	24 (301)	30 (184)
TOTALS	1000	260 (9403)	177 (2854)	117 (1413)	98 (1084)

* The animals that summer in the Pipestone River were found to be part of the herd that winters in the Red Deer River region.

( ) = Total number of animals counted.

population in the region is summarized in Figure 3.1. It involved 52-138 km of mountain travel (Table 3.2), and a minimum cumulative vertical movement of 2,000 m.

Details of distribution and movements are presented in Appendix B.

3.3.1. Winter distribution (December-April).

In winter, wapiti were mostly found outside Banff National Park.

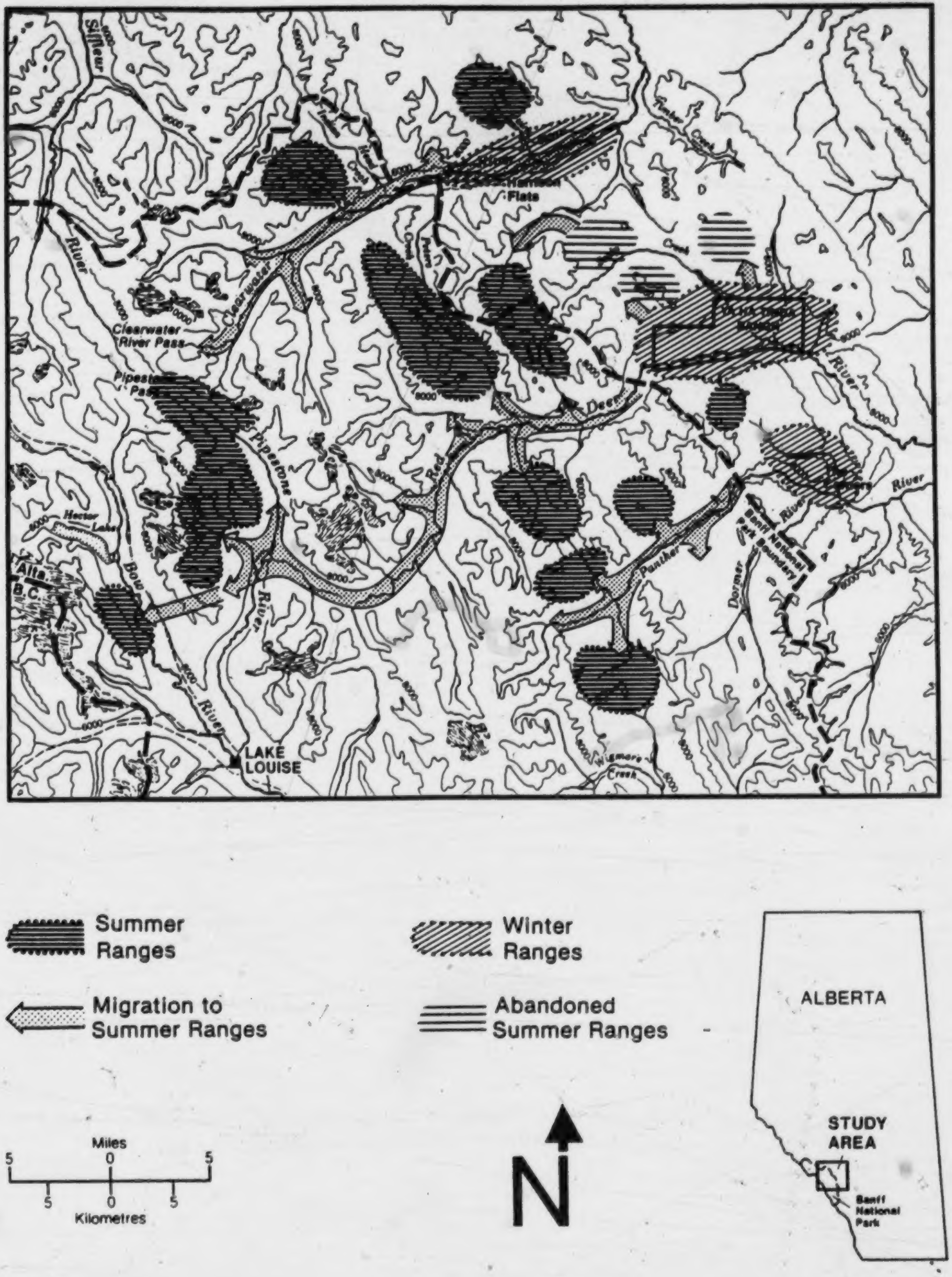
Within the Red Deer River drainage, large "nursery" herds, comprised of cows, calves and juveniles (50-400 individuals), wintered on the extensive open grassland in the Ya Ha Tinda Ranch, while smaller herds and single bulls were observed in the surrounding areas. Only a few wapiti (approx. 30) remained throughout the winter in Banff National Park.

Along the Clearwater River, wapiti made extensive use of several open meadows and south facing slopes 2-12 km outside the Park boundary. The use of ranges in the National Park was limited.

Within the Panther River watershed, wapiti wintered in significant numbers both inside and outside Banff National Park. Outside the National Park, most observations were recorded in the Corners region. In Banff National Park, wapiti wintered throughout the Panther River valley.

During special winter hunting seasons (Jan.-Feb. 1977 and 1978), wapiti returned to Banff National Park and heavily used

FIGURE 3.1. Migratory patterns of wapiti in the Red Deer-Panther-Clearwater region (1977-1980).


Siffleur River
Harrison Flats
Clearwater
Clearwater River Pass
Pipestone Pass
Pipestone
Red Deer River
Ya Ha Tinda Ranch
River
Hector Lake
Bow River
Alta.
B.C.
LAKE LOUISE
Panther River
Dormer River
Banff National Park Boundary
Wigmore Creek
Summer Ranges
Winter Ranges
Migration to Summer Ranges
Abandoned Summer Ranges
Miles
5
0
5
5
0
5
Kilometres
N
ALBERTA
STUDY AREA
Banff National Park

Base map adapted from Dept. of Energy, Mines and Resouces, Canada.

Table 3.2. Distance between summer and winter ranges of 18 wapiti collared on the Ya Ha Tinda Ranch (1977-1979).

	Linear distance (km)			Minimum travel distance* (km)		
N**	Average	Range	S.D.	Average	Range	S.D.
21	37.6	17.5-57.5	14.1	49.8	26.5-67.5	17.9

Note: * Minimum travel distance along river valleys.
** During the study two animals used three different summer ranges.
S.D. - Standard Deviation

small grassland meadows along the Red Deer River valley. Other herds moved from the Corners and the Ya Ha Tinda Ranch onto surrounding high elevation ranges (Morgantini and Hudson 1985). However, in 3-5 days following the hunting seasons, the animals re-established their habitual range outside the National Park.

3.3.2. Summer Distribution (July-August)

During July and August 1977, 1978 and 1979, a total of 1,417 wapiti were counted in 118 observations. Collared animals were present in 66 observations.

In the summer, wapiti were mostly found within the boundary of Banff National Park, widely dispersed over some 1,600 km^2 of mountainous terrain. Of a total of 22 animals collared in winter on the Ya Ha Tinda Ranch, 10 were found to summer in the Pipestone-Lake Louise area, seven in the Red Deer River watershed, one along the Panther River, and two in the Clearwater River region. Two more animals were never located and were presumed dead.

Large herds (30-70 animals), with well defined movement patterns, used high subalpine and alpine ranges at the headwaters of several creeks tributary to the Red Deer, Panther and Clearwater Rivers. Approximately 200-250 animals, more than 30% of the Ya Ha Tinda Ranch winter herd, summered in the Pipestone-Lake Louise-Bow River valley area. However, small herds of cows (1-10 animals) and bulls were found throughout the National Park, wherever favorable habitat was available. Occasionally, wapiti were also observed along the main river valleys while travelling from or to their summer ranges.

Between 1977 and 1979, only approximately 70 wapiti, less than 10% of the total winter population of the region, summered outside Banff National Park. They mostly consisted of small herds of cows and calves and isolated bulls. The highest number (30 individuals) was observed in the Clearwater watershed.

In the summer of 1977, a herd of 34 animals (five bulls, 21 cows with two collared individuals and eight calves) remained on the Ya Ha Tinda Ranch until the third week of July. When disturbed by hikers and trail riders, the animals first moved onto the surrounding slopes and ridges where they remained until the first week of August. After continuing harassment by 4x4 vehicles, the animals left the region and moved to alpine ranges, 24 km distant, in Banff National Park.

3.3.3. Spring and fall migrations

With the exception of a small non-migratory herd (5-15 animals), wapiti exibited well-defined seasonal migrations between winter and summer ranges. Their minimum travel distance from winter ranges to summer ranges located in Banff National Park varied from 26 to 68 km, with an average distance of 50 kilometers (Table 3.2).

Spring migrations consisted of an initial gradual shift from winter ranges to ranges located farther west along the major river valleys (spring "intermediate" ranges). This movement was later followed by a rapid migration to high elevation ranges. The timing of spring migrations showed great variation. Even though some animals were observed leaving their winter range in early May, most of the movements occurred during the second half of May and in early June. Spring migrations overlapped with the calving season (May 25 - June 5). Calving was observed throughout the area and it appeared to slow spring movements.

Fall migrations toward winter ranges occurred between September and November. Initially, they consisted of a shift onto lower elevation ranges along the major river valleys (intermediate ranges). This movement coincided with early snowfall (Table 3.3). Temporary returns to higher elevation ranges during warm fall weather, 1-2 days following snowfall, were also observed. By the end of September, most of the wapiti population was found on intermediate ranges. However, during October, instead of gradually shifting onto winter ranges, wapiti concentrated on intermediate ranges just inside Banff National Park.

Differently from the Red Deer and Panther River herds, wapiti in the Clearwater River valley tended to move outside the National Park at an earlier date (early November).

Table 3.3. Elevational distribution of wapiti before, during, and after early snowfalls in 1977 and 1978.

Date	Elevation (m) ($\bar{x} \pm$ S.D.)	Total snowfall at 1650 m	No. of observations
1977			
September 9-10	2181 ± 253a	0.0	6 (105)
September 13-16	1746 ± 102bc	15.0*	13 (93)
September 17-26	2028 ± 192ad	0.0	19 (131)
September 27-30	1741 ± 18bc	6.4**	15 (148)
1978			
September 11-17	2030 ± 194	0.0	8 (66)
September 18-19	1887 ± 101	13.0*	10 (78)
September 20-28	2077 ± 142	0.0	11 (134)

Values within columns followed by different letters are significantly different at $P<0.05$ (multiple range analysis).

* Snowfall over the entire period

** Snowfall on September 27.

( ) Total number of animals observed

3.3.4. Intermediate ranges

In spring and fall, wapiti used distinct ranges (intermediate ranges) located along the major river valleys, between winter and summer ranges. Intermediate ranges received extensive use in June and from September through November. The location and level of utilization depended on the date animals left their common winter range and on the distance between winter range and individual summer ranges.

Within the Red Deer watershed, animals that summered close to the Ya Ha Tinda Ranch winter range remained along the Red Deer River valley until early July. In contrast, the segment of the population with summer ranges in the Pipestone-Lake Louise area continued its gradual movement westward along the Red Deer and the Pipestone Rivers. Some of these animals left the Ya Ha Tinda Ranch in the middle of May and by early June had established their spring "intermediate" ranges (55 kilometers distant) along the Pipestone River. Others never established intermediate ranges, but, having left their winter range at a later date, used the entire month to gradually shift onto summer ranges in the upper Pipestone River.

Seasonal migrations along the Clearwater and the Panther River followed the same overall pattern. However, since most of the summer ranges in these watersheds (e.g. Indian Head Creek, Mallock Creek, upper Panther River and Harrison Lake area) are close to winter ranges, the majority of animals resided on intermediate ranges throughout the month of June (e.g. Mallock Creek and Sulphur Spring meadows). Along the Clearwater River, due to the vicinity of winter and summer ranges, wapiti that were found to summer outside Banff National Park (Lost Guide Creek) did not use any clearly definable intermediate range. Instead they tended to remain on winter ranges in spring and on summer ranges in the fall.

In the fall, intermediate ranges acted as major "staging areas" for large herds before their late fall-early winter (Nov.15-Dec.) movements onto winter ranges outside the National Park.

3.3.5. Range fidelity

Throughout the study region, wapiti exhibited predictable movements between ranges and a general tendency to return to the same ranges each year. The relatively low percentage of the total population collared (4% of the Red Deer River herd) did not allow a quantitative assessment of range fidelity. Nonetheless, the frequency of return of collared animals to specific summer ranges, and their return to a common winter range, are a clear indication of a well developed traditional behaviour (Table 3.4). This behaviour was further manifested in the use of the same migratory trails connecting different seasonal ranges.

Between 1977 and 1979, 11 of 18 collared wapiti returned to the same summer ranges. For eight of these animals, spring

Table 3.4. Number of collared animals that returned to the same ranges in successive years (1977-1980).

No. of successive years	Number of animals that returned to the same ranges	
	Summer ranges	Winter ranges
0	2	0
1	3	2
2	2	0
3	11	0
4	*	16

Note: The table does not include two animals that were never found and presumably died during the first winter and two animals that were shot by hunters outside Banff National Park.

* Systematic monitoring of summer ranges was carried out for only three years.

movements to their traditional ranges involved more than 60 km of travel across trails which would have allowed access to summer ranges closer to their wintering grounds.

In winter, 16 out of 18 collared wapiti returned to their common winter range for four successive years. Two males, trapped and collared as 10 month olds in March 1978, returned to the Ya Ha Tinda Ranch only the following winter. After moving to their habitual summer ranges in 1979, they were not relocated. Both animals were shot by hunters outside the National Park: one in the fall of 1980 along the Clearwater River, and the other in the fall of 1981 between the Panther and Red Deer Rivers.

3.4 Discussion

3.4.1. Migrations in the study region

The distribution of wapiti observed during this study is consistent with observations recorded by Banff National Park wardens between 1949 and 1976 (Banff National Park Files). The stability of regional movements and distribution is further confirmed by 11 additional ground surveys carried out between 1980 and 1983, and by more recent Banff National Park wildlife surveys (Skjonsberg 1988).

The concentration of wapiti on the Ya Ha Tinda Ranch reflects the availability of open winter ranges. The area represents less than 4% of the entire study region but, due to mild winter weather and mostly snow free conditions, it is an ideal winter range for most of the wapiti population that summers in northern Banff National Park. Winter ranges along the Panther and the Clearwater rivers offer significantly less open winter range (Morgantini and Russell 1983) and indeed support smaller number of animals.

In this typical northern mountain environment, wapiti appear to have adjusted to strong environmental fluctuations by rapid shifts from low elevation winter and intermediate ranges (1,500-1600 m) to high summer ranges (2,100-2,400 m), and *vice versa*. However, the location of summer ranges and range fidelity indicate that tradition (learned behaviour) plays a major role.

The significance of tradition has been emphasized by Wynne-Edwards (1962). There is ample evidence that wapiti return to the same ranges year after year and, in doing that, may use the same trails (Adams 1982).

The migration of approximately 200 animals from the Ya Ha Tinda Ranch to summer ranges north of Lake Louise and in the upper Pipestone River cannot be explained solely in terms of adaptation to local conditions. Migrating to summer ranges north of Lake Louise, for instance, involves an initial travel of 40 km along the Red Deer River valley to an elevation of 2100 m, then a downward movement of 25 km to an elevation of 1700 m and a final 2-3 km climb toward high elevation meadows.

All along the route there are well established trails to summer ranges significantly closer to the Ya Ha Tinda Ranch. These ranges were already used by animals from the same winter herd.

I can only think of two obvious explanations for this long range migratory behaviour. Yearly westward movements may reflect the original gradual dispersal (westward) and colonization of the region by an initial group of animals wintering on a common winter range outside Banff National Park. Conversely, the entire migratory pattern may be a vestige of the original dispersal of wapiti from the Bow River Valley. Historical evidence and this study tend to support the latter interpretation.

3.4.2. Original dispersal

In the early 1900s, wapiti had almost disappeared from the Canadian Rocky Mountains as a result of severe winters and indiscriminate hunting (Millar 1915, Stelfox 1964, Soper 1970). The present population is believed to have originated from the release of about 245-251 animals from Yellowstone National Park into Banff National Park, mostly along the Bow River valley, between 1917 and 1920 (Lloyd 1927, Green 1946). It has been suggested that this introduced stock interbred with the few remnant native wapiti and with wapiti moving into Banff National Park from British Columbia (Holroyd and Van Tighem 1983:416). The population rapidly increased and colonized adjacent valleys. Historical records show a gradual dispersal south-east into the Cascade River valley (1925), along the Panther River (1927) and Snow Creek (1931) (Banff National Park Files). These records, and the existence of well established trails from Wigmore-Cascade area into the Panther and the Dormer Rivers, suggest that wapiti dispersing from the Bow River valley reached the Panther River by following the Cascade River and then Wigmore Creek. The shift to the Red Deer River valley may have occurred in the summer across Snow Creek or, in winter, through the lower Dog Rib Creek.

The presence of wapiti from Kootenay National Park in the Red Deer River herd (this study: Appendix B), and the well established migratory pattern from the Pipestone to the Red Deer River, point to a second dispersal route. In the north-eastern section, wapiti were first reported in 1930 along Mosquito Creek, in 1936 along the Saskatchewan River and in 1942 along the Pipestone River (Banff National Park Files). At the time some wapiti from summer ranges in the upper Pipestone River may have travelled east along Little Pipestone River into the upper Red Deer River valley. The winter range on the Ya Ha Tinda Ranch may have been encountered by chance during downward movements along the Red Deer River valley. This movement may have been facilitated by the presence of a few wapiti remnant from the native population.

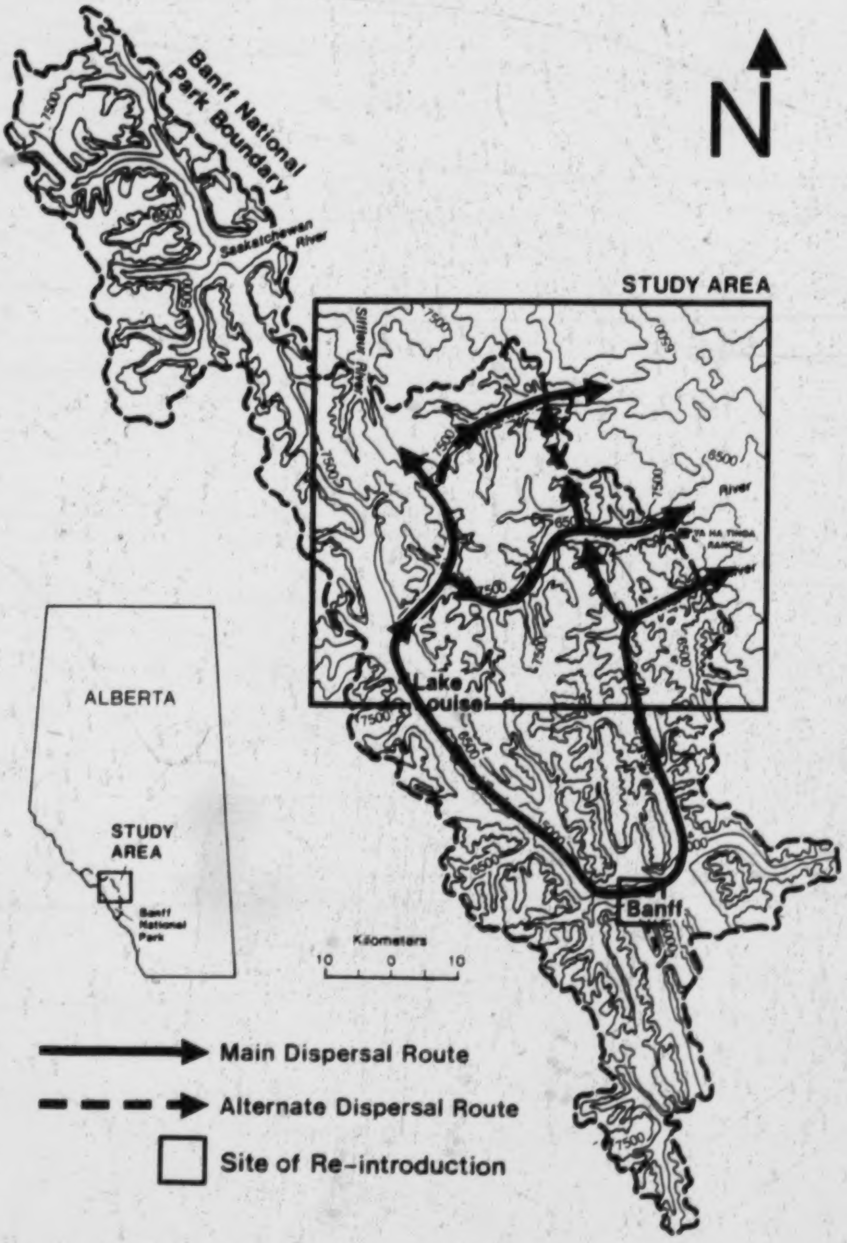
In comparison with the Panther and the Red Deer Rivers, access to the Clearwater River from the Bow River valley is limited. Dispersal and colonization may have occurred from the Sifleur River or from the lower Red Deer River valley.

The original dispersal of wapiti in the Red Deer-Panther-Clearwater region, as suggested by this study, is presented in Figure 3.2.

3.4.3. Migrations and the "familiar area" hypothesis

The dispersal of wapiti from their site of reintroduction and the present day migratory pattern in the region conforms to the theory of seasonal return migrations within familiar areas as developed by Baker (1978). The familiar area is defined as "the portion of the lifetime range from any point in which an animal is capable of finding its way to any other point" (Baker 1978:378). It is initially established during the course of successive exploratory movements (Baker 1978) and is largely maintained or extended through social communication within family units (cow-calf; Murie 1951) or through association of inexperienced with experienced animals. It has been suggested that migratory ungulates have several seasonal home ranges connected by travel routes (Geist 1971). However, the concept of familiar area differs from the concept of home range defined as "...the area over which an animal normally travels in pursuit of its routine activities" (Jewell 1966). A "familiar area" includes territory where habitats

FIGURE 3.2. Original dispersal of wapiti in the Red Deer-Panther-Clearwater region, as proposed by this study.


N
Banff National Park Boundary
Saskatchewan River
STUDY AREA
Siffleur River
7500
6500
River
YA HA TINDA RANCH
Lake Louise
Banff
ALBERTA
STUDY AREA
Banff National Park
Kilometers
10
0
10
Main Dispersal Route
Alternate Dispersal Route
Site of Re-introduction

Base map adapted from Holroyd and VanTighem, 1983.

were experienced by the animals, but, because of low suitability, have not been consistently visited since (Baker 1982). The concept of "familiar area" is similar to the concept of "lifetime range" proposed by Jewell (1966) as "the total area with which an animal has become familiar, including seasonal home ranges, excursions for mating, and routes of movement".

In the study area, exploratory and/or dispersal movements may have gradually led to the establishment of fairly separated familiar areas. The apparent inter-mingling between herds inhabiting different watersheds (Appendix B) and the occasional shift of animals from one herd to the other, may reflect a continuing process of extension of the familiar area of the individuals involved. The summer movements of herds from summer ranges outside Banff National Park to summer ranges in the Park following human disturbance (Appendix B), suggest that at least some wapiti are familiar with a region significantly larger than the one they are inhabiting.

3.4.4. Adaptive significance of migratory patterns

The significance of migratory behaviour in wapiti has been related to a large array of biotic and physical environmental features. In the Panther-Red Deer-Clearwater region, the presence of wapiti on seasonal ranges coincided with a period of high quality forage (Chapter 4). However, despite numerous apparent benefits, migratory behaviour is neither a pattern present in all wapiti populations nor, within the same population, in every individual. In the study region, a very secretive and small herd (5-15 individuals) remained on its winter range throughout the year. The spring-summer movements of a larger herd away from its winter range onto immediately adjacent high elevation ranges, and then toward distant regions, was due to human disturbance (Appendix B). It is reasonable to assume that the herd would have remained on winter range or in its immediate vicinity if it had not been harassed. It is known that migratory patterns can be determined and shaped by human disturbance (Altmann 1956, Harper et al. 1967, Flook 1970). It is also worth noting that 25 km east of the Ya Ha Tinda Ranch winter range, outside the front ranges of the Rocky Mountains, a herd of some 50 individuals are year round inhabitants of a region of forested hills interspersed with open slopes, muskegs and small, grassy meadows. The herd originated from 10 animals captured in Jasper National Park and released in the area in 1972-73. Even though these animals were originally part of a migratory population, they did not retain their migratory habits. While two animals travelled west and joined the main migratory Red Deer River herd, others that survived poaching and native hunting, successfully adjusted to the local seasonal environment.

3.5 Conclusions

Based on the behaviour of wapiti in the study region and on the existing knowledge of wapiti migratory habits, I see little evidence to suggest that the migratory behaviour of wapiti is an adaptation. Rather, it can be seen as expression of a behavioural pattern that can vary from local shifts in habitat use, to long range movements. It appears to be an adaptive strategy that allows each individual or group to choose among different alternatives, in order to variously adjust to environmental conditions, as determined by physiology and as shaped, through social communication, by learning and experience.

3.6 Literature cited

ADAMS, A. W. 1982. Migration. Pages 301-322 in: J. W. Thomas and D. E. Toweill eds. Elk of North America. Ecology and management. Stackpole Books, Harrisburg, Pa.

ALTMANN, M. 1952. Social behavior of elk, Cervus canadensis nelsonii, in the Jackson Hole area of Wyoming. Behavior 4: 116-143.

ALTMANN, M. 1956. Patterns of herd behavior in free ranging elk of Wyoming, Cervus canadensis nelsonii. Zoologica 41: 65-71.

ANDERSON, C. C. 1958. The elk of Jackson Hole. Bull. 10. Wyoming Game and Fish Comm. Laramie, Wyo. 184pp.

BAKER, R. R. 1978. The evolutionary ecology of animal migrations. Hodder and Stoughton, London. 1012pp.

BAKER, R. 1982. Migration. Paths through time and space. Hodder and Stoughton Ed. Ltd. London. 248pp.

BOYD, R. J. 1970. Elk of the White River Plateau, Colorado. Colorado Div. Game, Fish and Parks. Tech. Bull. 25. Denver. 126pp.

BRAZDA, A. R. 1963. Elk migration patterns and some of the factors affecting movements in the Gallatin River Drainage, Montana. J. Wildl. Manage. 17: 9-23.

CARBYN, L. N. 1974. Wolf predation and behavioral interactions with elk, and other ungulates in an area of high prey diversity. Can. Wildl. Serv. Rep. Ottawa. 233 pp.

COHEN, D. 1967. Optimization of seasonal migratory behavior. Am. Nat. 101: 5-17.

COX, G. W. 1968. The role of competition in the evolution of migration. Evolution 22: 180-192.

COWAN, I. McT. 1950. Some vital statistics of big game on overstocked mountain ranges. Trans. N. Am. Wildl. Conf. 15: 581-588.

CRAIGHEAD, J. J., G. Atwell, and B. W. O'GARA. 1972. Elk migrations in and near Yellowstone National Park. Wildl. Monogr. No. 29. 49 pp.

DALKE, P. D., R. D. BEEMAN, F. J. KINDEL, R. J. ROBEL, and T. R. Williams. 1965. Seasonal movements of elk in the Selway River Drainage, Idaho. J. Wildl. Manage. 29: 333-338.

DARLING, F. F. 1937. A herd of red deer. Oxford Univ. Press, London. 215pp.

FLOOK, D. R. 1970. A study of sex differential in the survival of wapiti. Can. Wildl. Serv. Rep. Ser. No. 11. Ottawa. 71pp.

GATES, C. and R. J. HUDSON. 1978. Energy costs of locomotion in wapiti. Acta Ther. 23: 365-370.

GEIST, V. 1971. Mountain sheep. A study in behavior and evolution. Univ. Chicago Press, Chicago. 383pp.

GEIST, V. 1978. Life strategies, human evolution, environmental design. Towards a biological theory health. Springer-Verlag, New York. 495pp.

GEIST, V. 1982. Adaptive behavioral strategies. Pages 219-278 in: J. W. Thomas and D. E. Toweill (Eds.), Elk of North America. Ecology and management. Stackpole Books, Harrisburg, Pa.

GREEN, H. U. 1946. The elk of Banff National Park. Banff National Park Rep. Banff, Alberta. 32 pp.

HARPER, J. A., J. H. HARN, W. W. BENTLEY, and C. F. YOKUM. 1967. The status and ecology of the Roosevelt elk in California. Wildl. Monogr. No. 16. 49pp.

HOLROYD, G. L. and K. J. VANTIGHEN. 1983. Ecological (biophysical) land classification of Banff and Jasper National Park. Vol. III: The wildlife inventory. Can. Wildl. Serv. Publ., Edmonton. 691pp.

JEWELL, P. A. 1966. The concept of home range in mammals. Symp. Zool. Soc. London 18: 85-109.

KNIGHT, R. R. 1970. The Sun River elk herd. Wildl. Monogr. No. 23. 66 pp.

LEEGE, T. A., and W. O. HICKEY. 1977. Elk-snow-habitat relationships in the Pete King drainage, Idaho. Wildl. Bull. No.6. Boise: Idaho Dep. Fish and Game. 23 pp.

LLOYD, H. 1927. Transfer of elk for restocking. Can. Field Nat. 41: 126-127.

MARTINKA, C. J. 1969. Population ecology of summer resident elk in Jackson Hole, Wyoming. J. Wildl. Manage. 33: 465-481.

MILLAR, W. N. 1915. Game preservation in the Rocky Mountains Forest Reserve. Dept. of the Int. Canada Forestry Branch Bull. No. 51. 69pp.

MORGANTINI, L. E. and W. B. RUSSELL. 1983. An assessment of three selected elk winter ranges in the Rocky Mountains Region. Wildlife Resources Consulting Ltd. Edmonton. Prepared for Alberta Fish and Wildlife Division. Edmonton. 265pp.

MURIE, O. J. 1951. The elk of North America. Stackpole Books, Harrisburg, Pa. 376pp.

SKINNER, M. P. 1925. Migration routes in Yellowstone Park. J. Mammal. 6: 184-192.

SKJONSBERG, T. 1988. Banff National Park. Eastern slopes wildlife study. 1984-1987. Banff National Park Files. Banff.

SOPER, J. D. 1970. The mammals of Jasper National Park, Alberta. Can. Wildl. Serv. Rep. Ser. No. 10. Ottawa. 80pp.

STELFOX, J. G. 1964. Elk in northeast Alberta. Land Forest Wildl. 6: 14-23.

STELFOX, J. G. 1974. Range ecology of rocky mountain bighorn sheep in canadian national parks. Can. Wildl. Serv. Rep. for Parks Canada. 234pp.

WARD, A. L., J. J. CUPAL, A. L. LEA, C. A. OAKLEY, and R. W. WEEKS. 1973. Elk behavior in relation to cattle grazing, forest recreation and traffic. Trans. N. Am. Wildl. Nat. Res. Conf. 38: 327-337.

WYNNE-EDWARDS, W. C. 1962. Animal dispersion in relation to social behaviour. Oliver and Boyd, Edinburg. 653pp.

4. FORAGE SELECTION

4.1. Introduction

4.1.1. Diet composition

Throughout North America, wapiti exhibit a wide variety of food habits and feeding behaviours. In a review of wapiti diets, Nelson and Leege (1982) listed 111 shrub and tree species, 76 grass and grasslike plant species and 142 forb, fern and lichen species. Of these, 72 shrubs and trees, 66 grasses and grasslike plants and 96 forbs, ferns and lichens were considered "valuable" or "highly valuable" forage plants based on whether they made up a major part of the diet or whether they were actively sought by the animals.

Altough wapiti prefer herbaceous plants to shrubs (Harper _et al_. 1967, Nelson and Leege 1982), forage selection appears to be largely dictated by forage availability, as determined by local environmental conditions. Hence, a plant species that is preferred in one area may not be selected on other ranges that support higher quality forage. The diverse diets that wapiti exhibit throughout their range reflect their capacity to adjust to and succesfully reproduce in markedly different environments, from climax shrublands in Alaska (Batchelor 1965) to dry chaparrals in Arizona (Bryant and Maser 1982) to rainy coastal forests in California (Harper _et al_. 1967). This adaptability can be ultimately related to the wapiti digestive system. Based on digestive anatomy and on diet composition, wapiti are classified as mixed feeders, to distinguish them from browsers (concentrate selectors) and grazers (roughage feeders) (Hoffman 1973, 1988). Mixed feeders can consume various forage types (grasses, browse, forbs) depending on seasonal quality and availability. Their rumen structure retains fibrous forage for longer periods (Hoffman 1973), while the absorptive epithelium of the rumen can change in response to diet quality (Hoffman 1985).

4.1.2. Forage quality

Forage quality refers to the nutritional content of forage relative to animal requirements for maintenance, growth and reproduction (Dietz 1970, Nelson and Leege 1982). Nutrient content varies among forage species, and is affected by numerous edaphic and climatic factors such as soil depth, composition, moisture content, slope and aspect, environmental temperature, daylight, and precipitation (Oelberg 1956, Laycock and Price 1970, Cook 1972). Forage quality also varies with plant phenology. Most species are high in nutrients during the early stages of growth, but decrease in nutritional value as they mature (Cook 1972, Dietz 1970, 1972).

4.1.3. The nutritional significance of migrations

The nutritional significance of seasonal migrations has been the subject of speculation. It is known that plants from alpine tundra have a high nutrient content due to their rapid growth and compressed phenological stages (Bliss 1962, Klein 1965, Chapin et al. 1975, Johnston et al. 1968). Klein (1970) estimated a delay of 3-4 days in the onset of plant growth in spring for each 100 to 130 m increase in altitude. The nutritional advantage for bighorn sheep and deer to forage on high elevation ranges has been suggested by several authors (Klein 1965, 1970, Hebert 1973, Shackelton 1973, Oosenbrug and Theberge 1980, Hamr 1984). In red deer, migratory females gained more weight than sedentary animals of the same population (Langvatn and Albon 1986). Geist (1982) hypothesized that wapiti, as a northern species adapted to exploit areas of high vegetational productivity, should follow shifting lines of plant growth and migrate to alpine habitats to maximize energy intake and, hence, reproductive fitness.

This chapter examined seasonal food habits of wapiti in relation to changes in forage quality of three distinct seasonal ranges.

4.2. Methods

Diet composition was determined through the identification of plant cuticular fragments in composite fecal samples (Hansen et al. 1973, Todd and Hansen 1973). Every month, 20 samples of fresh wapiti pellets were randomly collected, oven-dried at 55° C for 48 h, and pooled in one composite monthly sample. Plant fragments were identified and enumerated by the Composition Analysis Laboratory, Colorado State University.

The fecal fragment analysis technique has several limitations (Putman 1984). Differential digestion of forage types may result in fecal fragment compositions where more digestible species (*e.g.* forbs in summer) are underrepresented. However, the cuticle is considered indigestible although fragments may become more difficult to discern. In this study, the diet composition of wapiti, as estimated through fecal analysis, is consistent with habitat utilization patterns, forage availability and with direct observation of animals feeding. This suggests that the results represent a reliable estimate of the food habits of wapiti in the region.

Range quality was assessed by collecting composite forage samples from seasonal ranges. Samples were obtained by clipping standing forage 2 cm above the ground from 10 randomly distributed 20 X 50 cm plots. Composite range collections were considered adequate for this study, as an efficient technique to assess overall range quality in areas with homogeneous plant composition when no prior information on food habits is available (Morgantini and Hudson 1985). Willow samples consisted of current annual growth.

Collections on alpine summer ranges were restricted to snow free months, July-September. The samples were dried and crude protein content (Kjeldahl N X 6.25) was determined using the macro-Kjeldahl technique (A.O.A.C. 1965). *In vitro* digestible dry matter (IVDDM) determination followed Tilley and Terry (1963) and Minson and McLeod (1972), as modified by Morgantini and Hudson (1985). Rumen inoculum was obtained from a fistulated wapiti steer maintained on a diet of pelleted aspen-barley concentrate, chopped alfalfa, and browse. The animal had *ad libitum* access to a tame grass pasture.

Fecal protein content was adopted as a crude index of diet quality (Lambourne and Reardon 1963, Cordova 1977, Mould and Robbins 1983, Renecker and Hudson 1985). Fecal lignin was used as a supplementary measure because it reflects the amount of woody material in the diet (Van Soest 1982). Every month, twenty fresh fecal samples were collected and frozen before they were oven-dried at 55 C for 48 hours. For analysis, composite samples were prepared by taking approximately 5 gm of material from each of five original samples. Fecal crude protein was determined using the macro-Kjeldahl method (A.O.A.C. 1965). Permanganate lignin was determined according to Van Soest (1976).

4.3. Results

4.3.1. Diets

The contribution of major plant groups to the diet of wapiti on seasonal ranges is summarized in Table 4.1.

On winter ranges, grasses made up 89.9 % of the diet. Rough fescue (Festuca scabrella) was the dominant grass species. On intermediate ranges (Chapter 3), the contribution of grasses decreased to 70.6 %, and browsing increased from 3.7 to 18.6 %. On summer ranges, wapiti diet shifted from grasses to shrubs. The contribution of willow increased from 10.5 to 88.6%, whereas grasses and forbs accounted for only 7.1% of the diet. Since animals were largely observed feeding on alpine tundra, it must be assumed that they were "browsing" on low growing species, such as arctic and snow willow, that were very abundant in the region.

In fall, after moving to lower elevation intermediate ranges, wapiti returned to a grass-dominated diet. Browsing decreased to 19.7% and mostly occurred on wolf-willow (Eleagnus commutata).

4.3.2. Forage quality

From October until May, crude protein and IVDDM of herbaceous plants (Table 4.2) from winter and intermediate ranges were not significantly (P>0.05) different. In June, however, when wapiti were on intermediate ranges, forage from

Table 4.1. Percent diet composition of wapiti on seasonal ranges in west-central Alberta, based on fragment analysis. January 1977-December 1978.

	Winter range (Dec.-May) n*=12		Interm.range (June) n*=2		Summer range (July-August) n*=4		Interm.range (Sept.-Nov.) n*=4	
	$\bar{x}$	se	$\bar{x}$	se	$\bar{x}$	se	$\bar{x}$	se
Grasses								
Fescue	88.2	0.61	56.6	11.9	0.4	0.05	64.7	10.2
Wild rye	0.6	0.08	7.8	4.7	1.7	0.36	3.6	0.77
Bluegrass	0.5	0.10	5.7	2.6	1.4	0.19	3.9	1.5
Other	0.6	0.06	0.4	0.3	0.5	0.17	0.2	0.07
Total	89.9	0.47	70.6	4.5	3.9	0.55	72.3	7.9
Sedges								
Total	4.2	0.13	6.4	1.4	2.4	0.71	3.5	0.58
Browse								
Willow	1.5	0.16	10.5	3.4	88.6	1.51	1.0	0.18
Other	2.2	0.22	8.9	0.6	0.3	.06	18.4	8.48
Total	3.7	0.27	19.4	4.0	88.9	1.57	19.7	8.30
Forbs								
Total	2.2	0.45	3.6	1.0	2.6	0.64	4.5	0.92

* Each monthly sample represents a composite sample of twenty pellet groups.

Table 4.2. Percent crude protein content and IVDDM of composite range samples from seasonal ranges. January 1977-December 1978.

	Winter range				Intermediate range				Summer range			
	CP		IVDDM		CP		IVDDM		CP		IVDDM	
	$\bar{x}$	se	$\bar{x}$	se	$\bar{x}$	se	$\bar{x}$	se	$\bar{x}$	se	$\bar{x}$	se
Dec.-Apr.	3.6	0.06	67.4	0.22	3.7	0.10	67.9	2.16	*		*	
May	7.5	0.28	71.1	0.85	6.8	0.32	72.8	0.88	*		*	
June	10.5a	0.48	78.2a	1.45	13.5b	0.42	81.6b	1.70	*		*	
July-Aug.	8.2a	0.37	72.6a	1.66	10.2b	0.33	76.9b	1.15	13.8c	0.63	71.4a	4.81
Sept.-Nov.	4.3a	0.59	65.1a	0.91	5.2b	0.36	69.4b	1.46	7.8c	0.72	66.2a	1.31

* Ranges not accessible due to deep snow
Values for a parameter within a row followed by different letters are significantly different at $P<0.05$

these ranges had a significantly higher protein content ($P<0.0003$) and dry matter digestibility ($P<0.005$) than that found at the same time on winter ranges. At the time, summer ranges were largely unavailable due to extensive snowdrifts and late snow melt.

In July, while forage crude protein from both winter and intermediate ranges decreased with advancing maturity, the vegetation on summer ranges was in full seasonal growth. Crude protein content of herbaceous plants was higher than on intermediate and winter ranges. However, no significant change in digestibility values between intermediate and summer ranges was recorded.

From August to October, protein content of alpine forages decreased but remained higher than that on intermediate ranges. In the autumn, crude protein content and digestibility of herbaceous plants on intermediate ranges was higher than that on winter ranges.

Throughout the year on all seasonal ranges, crude protein of willow species (Table 4.3) was consistently higher than that of herbaceous plants. In contrast, _in vitro_ digestibility was consistently lower, ranging from a winter low of 47.7 % on winter ranges to 63.4 % in July on summer ranges.

4.3.3. Fecal indices

Fecal crude protein followed a seasonal cycle parallel to that observed in forage protein from seasonal ranges (Figure 4.1). During both years of study, fecal protein from October to May ranged between 8.06 and 10.94 %. In summer, when wapiti were on alpine ranges, it rose to over 22 %, sharply decreasing afterwards. Total nitrogen content of wapiti feces was correlated ($r^2=.90$; $P<0.001$) with the estimated nitrogen content of their diet (Figure 4.2).

Fecal lignin content was found to be highly correlated with the amount of browse in the diet (Figure 4.3). In 1977, fecal lignin ranged from an average of 13.5 % (± 1.1) in winter to 21.5 % (± .20) in summer, and, in 1978, from 14.5 % (± .40) to 24.5 (± .3).

Seasonal fluctuations in fecal lignin content paralleled changes in dietary browse content and were opposite to changes in fecal ash content (Figure 4.4).

4.4. Discussion

4.4.1. Diet quality

The seasonal cycle of forage quality on seasonal ranges reflects the natural cycle of plant phenology, i.e. a sharp decline in protein and digestibility after the early growth stages (Moen 1973). Crude protein content of forage species in the study region are consistent with data presented by Johnston and Bezeau (1962), Johnston *et al*. (1968) and Hebert (1973).

Table 4.3. Percent crude protein content and IVDDM of willow leaves and twigs from seasonal ranges. January 1977-December 1978.

	Winter range				Intermediate range				Summer range			
	CP		IVDDM		CP		IVDDM		CP		IVDDM	
	$\bar{x}$	se	$\bar{x}$	se	$\bar{x}$	se	$\bar{x}$	se	$\bar{x}$	se	$\bar{x}$	se
Dec.-Apr.*	8.8	0.08	51.1	1.13	8.0	0.30	49.1	0.36	-		-	
May***	9.6a	0.03	52.9a	0.93	8.6b	0.20	48.7b	1.03	-		-	
June***	19.4a	0.70	61.5	2.06	17.9b	0.04	57.7	1.99	-		-	
July-Aug.**	13.1a	1.00	61.9	1.43	15.8b	0.10	60.1	0.35	16.8b	0.80	61.8	1.17
Sept.-Nov.*	9.9a	3.90	55.4	4.35	7.8b	0.60	55.1	2.02	9.6a	0.45	57.5	0.38

- Ranges not accessible due to deep snow
Values for a parameter within a row followed by different letters are significantly different at $P<0.05$
* twigs only; ** leaves only; *** leaves and twigs.

FIGURE 4.1. Crude protein in forage and feces
from different seasonal ranges
in the Red Deer-Panther-Clearwater region
along the east slopes of the Rocky Mountains
(1977-1978).

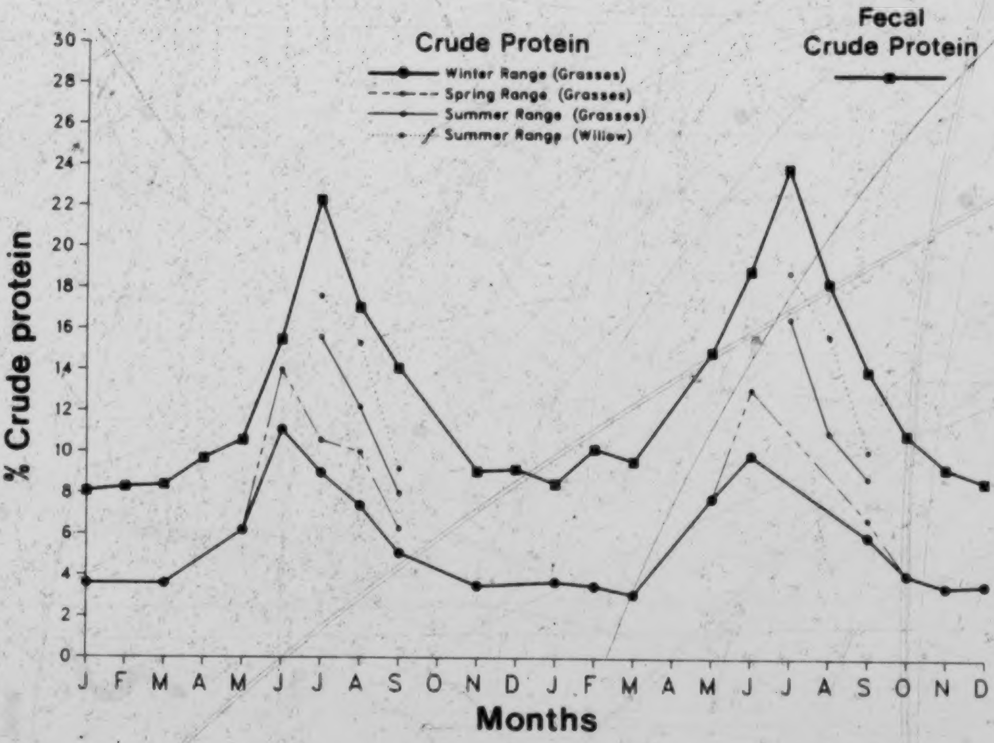

Crude Protein
Winter Range (Grasses)
Spring Range (Grasses)
Summer Range (Grasses)
Summer Range (Willow)
Fecal
Crude Protein
% Crude protein
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
J F M A M J J A S O N D J F M A M J J A S O N D
Months

FIGURE 4.2. Relationship between fecal nitrogen and estimated nitrogen content of diet of wapiti in the Red Deer-Panther-Clearwater region along the east slopes of the Rocky Mountains (1977-1978).

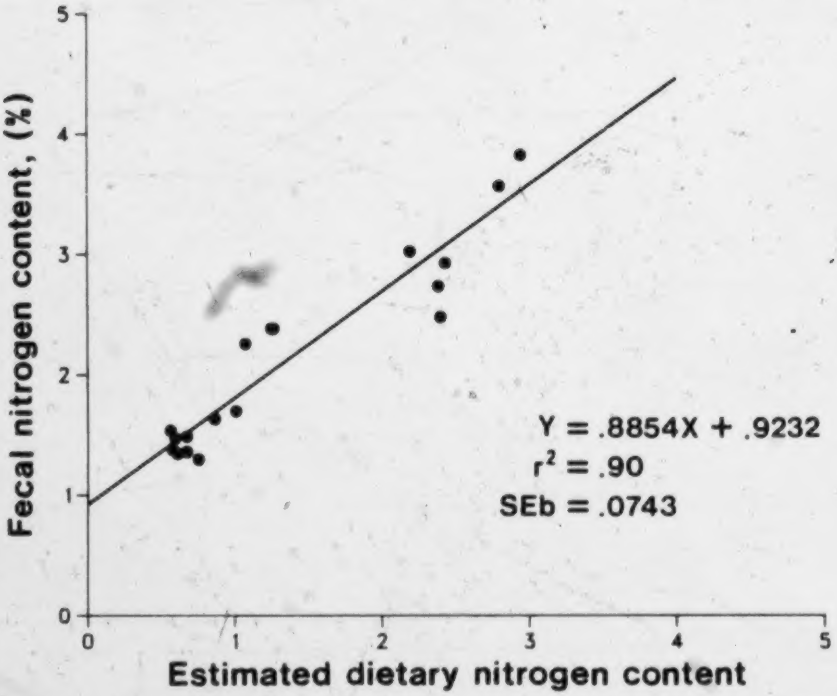

Fecal nitrogen content, (%)
5
4
3
2
1
0
0
1
2
3
4
5
Estimated dietary nitrogen content
Y = .8854X + .9232
r^2 = .90
SEb = .0743

FIGURE 4.3. Relationship between fecal lignin and browse content of diet of wapiti in the Red Deer-Panther-Clearwater region along the east slopes of the Rocky Mountains (1977-1978).

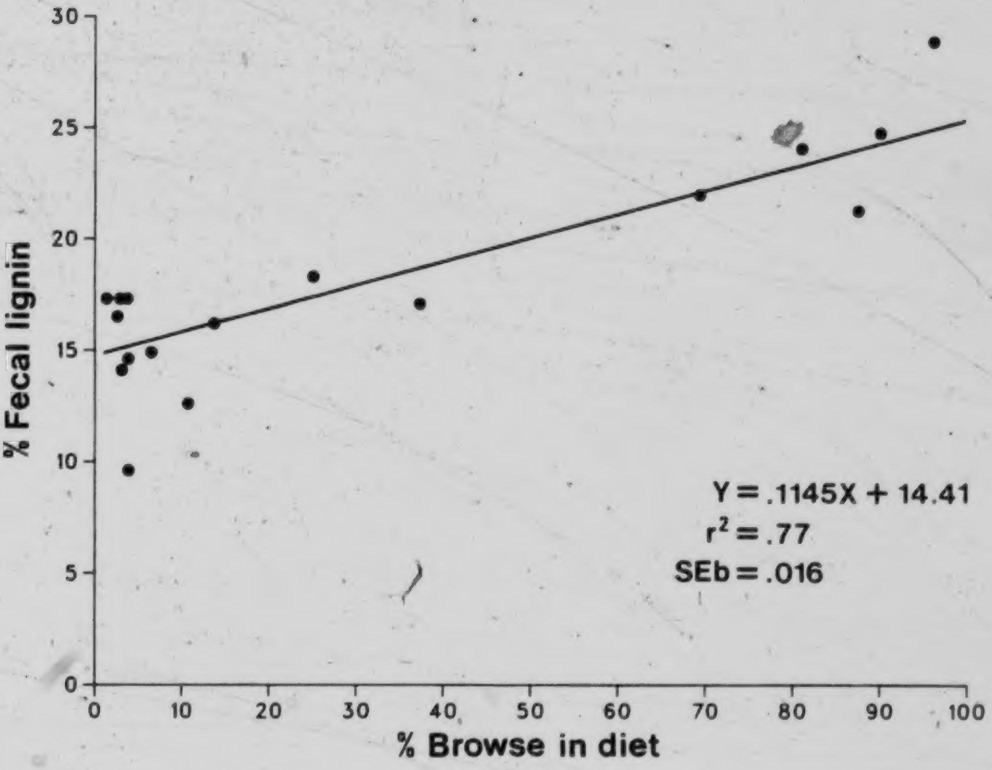
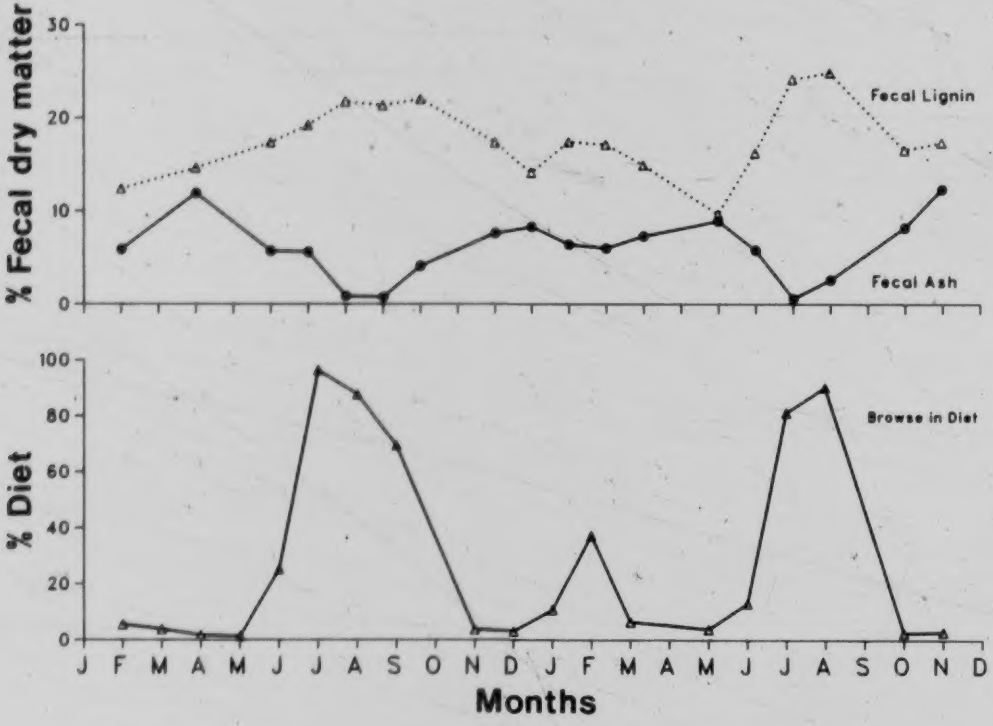

30
25
20
15
10
5
0
0
10
20
30
40
50
60
70
80
90
100
% Fecal lignin
% Browse in diet
Y = .1145X + 14.41
r^2 = .77
SEb = .016

FIGURE 4.4. Fecal lignin, fecal ash, and browse dietary component of wapiti in the Red Deer-Panther-Clearwater region along the east slopes of the Rocky Mountains. (1977-1978).


% Fecal dry matter
30
20
10
0
Fecal Lignin
Fecal Ash
% Diet
100
80
60
40
20
0
Browse in Diet
J F M A M J J A S O N D J F M A M J J A S O N D
Months

Within the Panther, Red Deer and Clearwater regions, the timing of wapiti use of intermediate (June) and summer (July) ranges coincided with a period of higher forage quality in those areas.

In winter, rough fescue made up a large portion of the diet. However, despite its high digestibility, rough fescue is a poor source of nitrogen. Crude protein content at a weathered stage ranges from 2.6% (Morgantini and Hudson 1985) to 4.2 % (Johnston and Bezeau 1962). Dietary protein requirements for wapiti in winter are believed to range between 5% and 7% (Hobbs et al. 1981, Nelson and Leege 1982). Crude protein content (± SE) of composite range samples collected during this study averaged 3.8% (± 0.19) on intermediate ranges in October and November and 3.6% (± 0.03) on winter ranges from December to April. Nitrogen requirements may be partially met by nitrogen recycling, by selective foraging for plant parts with a higher nitrogen content or by an increase in dry matter intake (Nelson and Leege 1982). Nonetheless, this study indicates that wapiti inhabiting mountain regions of west-central Alberta likely face inadequate forage nitrogen for seven months of the year.

Nelson and Leege (1982) estimated that forage crude protein concentrations required by an adult wapiti cow in spring and summer for maintenance and lactation would increase from 5 % in May to 11 % in August. During this study, wapiti, by grazing first on intermediate ranges and then on alpine ranges, had access for three months to forage containing over 13% crude protein.

The importance of shrubs in the summer diet of wapiti has been reported by Hash (1973) in Idaho and Bohne (1974) in Montana. During this study, wapiti on alpine ranges shifted to a browse-dominated diet. Fecal analysis might have overestimated willow due to its lower digestibility (Pulliam and Nelson, 1979). However, a major increase in browsing is also indicated by the increase of fecal lignin content and decrease in fecal ash residue.

There is limited information on the nutritional quality of alpine willows. In arctic environments, the cell solubles of some willow species (Salix arctica, Salix lanata, Salix pulcra) are comparable to those of forbs and grass-like plants (70-80%) (Person et al. 1980). In this study, while alpine willows (arctic and snow willow) had a significantly higher crude protein content than grasses, they were less digestible. The low in vitro digestibility could reflect the lack of adaptation of the rumen inoculum as shown by Person et al. (1980). In their study, inoculum from tame reindeer resulted in 52.6% digestibility as compared to 71.5% for caribou inoculum obtained from free ranging animals. The difference was related to a different dietary regime. The concentration of secondary metabolites, which varies among plant species, may also affect in vitro digestibility by limiting microbial fermentation (White and Trudell 1980).

During this study, fecal lignin was significantly higher in summer than in winter. Higher fecal lignin in summer indicates higher dietary lignin content and, hence, lower diet digestibility (Van Soest 1982). However, through the early stages of plant growth, lignin only partially reduces the digestibility of cell wall constituents (Choo et al. 1981). Further, dietary lignin may increase the rate of forage passage through the digestive tract by enhancing particle breakdown and stimulating rumination (Mertens 1973, Ulyatt et al. 1986, Renecker 1987). Wapiti, as mixed feeders, can adjust to changes in forage quality depending on local environmental conditions (Hoffmann 1985). On alpine ranges, by shifting their diet to willow leaves and current year twigs, wapiti appear to select for a diet of high crude protein content. The eventual decrease in digestibility may be compensated by increased intake and rate of passage.

4.4.2. Fecal nitrogen

The relationship between fecal nitrogen content and dietary nitrogen content, and its value for evaluating diet quality of free ranging ungulates, have been reviewed by Robbins (1983). In this study, the regression coefficient between fecal nitrogen and estimated diet nitrogen (browse and herbaceous plant components) differed markedly from that reported by Mould and Robbins (1981) for wapiti. The prediction of dietary nitrogen from fecal nitrogen by using the Mould and Robbins (1981) equation yields unrealistic values of diet crude protein content (N x 6.25) of 35.3 % and 39.5 % in July 1977 and 1978, respectively. The regression coefficient obtained in this study was closer to that reported by Renecker and Hudson (1985) for moose, and it may indicate, as suggested by these authors, a high level of total fecal nitrogen and of metabolic fecal nitrogen (MFN) excretion for browsers. The low nitrogen content of the wapiti diet on winter ranges, and the high level of browsing in the summer, support this suggestion. In winter, a large component of total fecal nitrogen may be of metabolic origin, while in the summer MFN may be complemented by undigested dietary nitrogen.

4.4.3. Adaptive significance of dietary changes

Ungulates living in northern environments depend on summer forage of high nutritional quality for reproduction and growth and to compensate for nutritionally inadequate winter diet. Weight loss during the winter can ultimately determine survival and reproductive success (Thorne 1976, White 1983). Hence, herbivores "should" adopt a feeding "strategy" which will maximize summer growth (Geist 1982).

In the study region, wapiti likely face inadequate forage protein content for seven months of the year. In the remaining four to five months, the animals must engage in the following energy-demanding activities: completion of gestation, calving, lactation, replacement of body reserves, weight gain and breeding. The benefits of following early plant growth that has the highest nutrient content, appear evident. However, it is also possible that the animals move to seasonal ranges for other reasons (such as insect avoidance, interspecific competition, learned behaviour, etc.), and that the nutritional benefits are totally or partially coincidental. In such a case, the fact that migratory routes in spring follow early plant growth could reflect a pre-adapted behaviour, instead of being an adaptation to northern environments. It should also be noted that in the study region wapiti that follow a long, up and down route to their summer range, forage at times in areas of lower forage quality than the area they just left. For example, in spring, wapiti that summer in the Pipestone River region, have to travel through and forage on summer ranges (Red Deer River headwaters) where the vegetation is still in a dormant stage.

Due to the absence of a significant number of non-migratory wapiti in the study region, I could not assess whether wapiti summering on winter ranges or in their vicinity were on a poorer diet and, hence, were entering winter in poorer conditions. However, even assuming that non-migratory wapiti consumed poorer quality summer forage, it is questionable whether the theoretical lowering of reproductive performance would be so significant as to affect the average reproductive success of individuals or populations. Only in the latter case, would the cost of long range migrations be warranted and, hence, would the feeding strategy associated with migrations be a selective trait. The existence of an apparently healthy, non-migratory wapiti population outside the study region suggests that foraging on high elevation ranges is not necessary for maintenance, growth and reproduction. Wapiti may be able to meet nutritional requirements through dietary changes, increased intake, higher selectivity or digestive adjustments.

4.5. Conclusions

Seasonal changes in diet composition and quality suggest that the feeding strategy of wapiti in winter consisted of maximizing digestible energy intake (Morgantini and Hudson 1985). Conversely, in summer, the animals selected for a diet with a high nitrogen content, despite the apparent lower dry matter digestibility.

Wapiti migrations onto spring and summer ranges in the Panther-Red Deer Clearwater region in west-central Alberta coincided with periods of high quality forage. Notwithstanding the nutritional benefits, it cannot be concluded from this study that foraging on distant summer ranges is an adaptation to seasonal environments.

4.6. Literature cited

A.O.A.C. 1965. Official methods of analysis. 10th ed. Association of Official Agricultural Chemists, Washington, D.C. 957pp.

BATCHELOR, R. F. 1965. The Roosevelt elk in Alaska - its ecology and management. Alaska Dept. Fish and Game, Juneau. 37pp.

BLISS, L. C. 1962. Adaptations of arctic and alpine plants to environmental conditions. Arct. 15: 117-144.

BOHNE, J. R. 1974. Food habits, seasonal distribution, and habitat utilization of elk in the South Fork of Fish Creek, Lolo National Forest, Montana. M. S. Thesis, Univ. Montana, Missoula. 197pp.

BRYANT, L. D., and C. MASER. 1982. Classification and distribution. Pages 1-60 in J. W. Thomas and D. E. Toweill (Eds.), Elk of North America. Ecology and management. Stackpole Books, Harrisburg, PA.

CHAPIN, F. S. III, K. VAN CLEVE, and L. L. TIESZEN. 1975. Seasonal nutrient dynamics of tundra vegetation at Barrow, Alaska. Arct. Alp. Res. 7: 209-226.

CHAPIN, F. S. III, K. VAN CLEVE, and J. D. McKENDRICK. 1980. Seasonal movements of nutrients in plants of differing growth form in an Alaskan tundra ecosystem: implications for herbivory. J. Ecol. 68: 189-209.

CHOO, G. M., P. G. WATERMAN, D. B. McKEY and J. S. GARTLAN. 1981. A simple enzyme assay for dry matter digestibility and its value in studying food selection by generalist herbivores. Oecologia 49: 170-178.

COOK, C. W. 1972. Comparative nutritive value of forbs, grasses, and shrubs. in C. M. McKell, J. P. Blaisdell, and J. R. Goodin (Eds.), Wildland shrubs - their biology and utilization. USDA For. Ser. Gen. Tech. Rep. Int-1.

CORDOVA, F. T. Intake and nutritive value of forage grazed by cattle on fertilized and unfertilized blue grama rangeland. Ph. D. Thesis, New Mexico State University, Las Cruces. 213pp.

DIETZ, D. R. 1970. Animal production and forage quality: definition and components of forage quality. Pages 1-9 in Range and wildlife habitat evaluation-a research symposium. Misc. Publ. 1147. Washington, D.C.: USDA For. Serv.

DIETZ, D. R. 1972. Nutritive value of shrubs. Pages 289-302 in Wildland shrubs-Their biology and Utilization. USDA For. Serv. GRT INT-1, Ogden, Utah.

GEIST, V. 1982. Adaptive behavioral strategies. Pages 219-278 in J. W. Thomas and D. E. Toweill (Eds.), Elk of North America. Ecology and management. Stackpole Books, Harrisburg, Pa.

HAMR, J. 1984. Home range size of male chamois (Rupicapra rupicapra) in the Tyrolean Alps. Acta Zool. Fennica 171: 293-298.

HANSEN, R. M., D. G. PEDEN, and R. W. RICE. 1973. Discerned fragments in feces indicates diet overlap. J. Range Manage. 26: 103-105.

HARPER, J. A., J. H. HARN, W. W. BENTLEY, and C. F. YOCUM. 1967. The status and ecology of the Roosevelt elk in California. Wildl. Monogr. No. 16. Washington, D.C. The Wildlife Society. 49pp.

HASH, H. S. 1973. Movements and food habits of the Lochsa elk. M.S. Thesis. University Idaho, Moscow. 85 pp.

HEBERT, D. M. 1973. Altitudinal migration as a factor in the nutrition of bighorn sheep. Ph.D. Thesis, Univ. Brit. Col. Vancouver, 357pp.

HOBBS, N. T., D. L. BAKER, J. E. ELLIS, and D. M. SWIFT 1981. Composition and quality of elk winter diets in Colorado. J. Wildl. Manage. 45: 156-171.

HOFMANN, R. R. 1973. The ruminant stomach. E. Afr. Monogr. Biol. 2. East African Literature Bureau, Nairobi. 354pp.

HOFMANN, R. R. 1985. Digestive physiology of the deer - their morphological specialization and adaptation. in P. F. Fennessy and K. R. Drew (Eds.), Biology of Deer Production. Royal Soc. New Zeal. Bull. 22: 393-408.

HOFMANN, R. R. 1988. Morphophysiological evolutionary adaptations of the ruminant digestive system. in M. and A. Dobson (Eds.), Aspects of digestive physiology in ruminants. Cornell Univ. Press, Ithaca.

JOHNSTON, A., and L. M. BEZEAU. 1962. Chemical composition of range forage plants of the Festuca scabrella association. Can. J. Plant Sci. 42: 105-115.

JOHNSTON, A., L. M. BEZEAU, and S. SMOLIAK. 1968. Chemical composition and in vitro digestibility of alpine tundra plants. J. Wildl. Manage. 32: 773-777.

KLEIN, D. R. 1965. Ecology of deer range in Alaska. Ecol. Monogr. 35: 259-284.

KLEIN, D. R. 1970. Food selection by north american deer and their response to over utilization of preferred plant species. Pages 25-46 in A. Watson, (Ed.), Animal Populations in Relation to Their Food Sources. Ed. Brit. Ecol. Soc. Symp. 10., Blackwell Sci. Publ., Oxford.

LAMBOURNE, L. J., and T. F. REARDON. 1963. The use of chromium oxide and fecal nitrogen concentrations to estimate the pasture intake of merino wethers. Aust. J. Agric. Res. 14: 257-271.

LANGVATN, R., and T. F. ALBON. 1986. Geographic clines in body weight of Norwegian red deer: a novel explanation of Bergmann's rule? Holarct. Ecol. 9: 285-293.

LAYCOCK, W. A., and D. A. PRICE. 1970. Factors influencing forage quality: environmental influences on nutritional value of forage plants. Pages 37-47 in Range and Habitat evaluation-a research symposium. USDA For. Serv. Misc. publ. 1147. Washington, D.C.

MERTENS, D. R. 1973. Applications of theoretical and mathematical models to cell wall digestion and forage intake in ruminants. Ph.D. Thesis, Cornell University, Ithaca, N.Y. 187pp.

MINSON, D. J., and M. N. McLEOD. 1972. The in vitro technique: its modification for estimating digestibility of large numbers of tropical pasture samples. Division of tropical Pastures. Technical Paper No. 8. C.S.I.R.O. Australia.

MOEN, A. N. 1973. Wildlife ecology: an analytical approach.

W.H. Freeman and Co., San Francisco. 458pp.

MOULD, E. D. and C. T. ROBBINS. 1981. Nitrogen metabolism in elk. J. Wildl. Manage. 45: 323-334.

MORGANTINI, L. E., and R. J. HUDSON. 1985. Changes in diets of wapiti during a hunting season. J. Range Manage. 38: 77-79

NELSON, J. R., and T. A. LEEGE. 1982. Nutritional requirements and food habits. Pages 323-368 in J. W. Thomas and D. E. Toweill (Eds.), Elk of North America. Ecology and management. Stackpole Books, Harrisburg, Pa.

NIETFELD, M. T. 1983. Foraging behavior of wapiti in the boreal mixed-wood forest, central Alberta. M.Sc. Thesis. Univ. Alberta, Edmonton. 187pp.

OELBERG, K. 1956. Factors affecting the nutritive value of range forage. J. Range Manage. 9: 220-225.

OOSENBRUG, S. M., and J. B. THEBERGE. 1980. Altitudinal movements and summer habitat preferences of woodland caribou in the Kluane Ranges, Yukon Territory. Arct. 33: 59-72.

PERSON, S. J., R. G. WHITE and J. R. LUICK. 1980. Determination of nutritive value of reindeer-caribou range. Pages 224-239 in E. Reimers, E. Gaare, and S. Skjenneberg (Eds.), Proc. 2nd Reindeer/Caribou Symp., Roros, Norway, 1979. Direktoratet for vilt og ferskvannsfisk, Trondheim.

PULLIAM, D. E. Jr., and J. R. NELSON. 1979. Determination of digestibility coefficients for quantification of fecal analysis with elk. Pages 240-246 in M. S. Boyce and L. D. Hayden-Wing (Eds.), North american elk: ecology, behavior and management. Univ. Wyoming Press, Laramie.

PUTMAN, R. J. 1984. Facts from faeces. Mammal. Rev. 14: 79-97.

RENECKER, L. A. 1987. Bioenergetics and behaviour of moose (Alces alces) in the Aspen Boreal Forest. Ph.D. Thesis. Univ. Alberta, Edmonton. 265pp.

RENECKER, L. A. and R. J. HUDSON. 1985. Estimation of dry matter intake of free-ranging moose. J. Wildl. Manage. 49: 785-792.

SHACKELTON, D. M. 1973. Population quality and bighorn sheep

(Ovis canadensis canadensis). Ph.D. Thesis. Univ. Calgary, Calgary.

TILLEY, J. M. A., and R. A. TERRY. 1963. A two stage technique for the in vitro digestion of forage crops. J. Br. Grassl. Soc. 18: 104-111.

TODD, J. W., and R. M. HANSEN. 1973. Plant fragments in the feces of bighorns as indicators of food habits. J. Wildl. Manage. 37: 363-366.

ULYATT, M. J., D. W. DALLOW, A. JOHN, C. S. W. REID, and C. G. WAGHORN. 1986. The contribution of chewing, during eating and ruminating, to the clearance of digesta from the rumino-reticulum. Pages 498-515 in L. P. Milligan, W. L. Grovum and A. Dobson (Eds.), Control of digestion and metabolism in ruminants. Prentice-Hall, Inglewood Cliffs, N.J.

VAN SOEST, P. J. 1976. Development of a comprehensive system of feed analyses and its application to forages. J. Anim. Sci. 26: 119-128.

VAN SOEST, P. J. 1982. Nutritional ecology of the ruminant. O.&B. Books, Inc., Corvallis, Oregon. 374pp.

WHITE, R. G. 1983. Foraging patterns and their multiplier effect on productivity of northern ungulates. Oikos 40: 377-384.

5. HABITAT SELECTION

5.1. Introduction

5.1.1. Habitat selection and adaptation

Habitat selection by ungulates is a complex behavioural response to physical and biotic features of their environment.

Heredity plays a role in dictating habitat prefences (Wecker 1964). There is evidence that learning, experience and cultural transmission are also important (Andersen 1973, Geist 1971). Ultimately, however, habitat selection is determined by the distribution and abundance of critical resources (Arnold 1964, Brown and Orians 1970).

Eisenberg and Lockart (1972) noted that "...in general, an ungulate species has two major problems: to feed itself and to avoid being fed upon". To cope with these two basic requirements, and in order to maximize reproductive fitness, behavioural and non-behavioural characteristics have evolved in an adaptive complex (Leuthold 1977) of which habitat selection is only one expression. The distribution and occupational pattern of an ungulate reflect its size, morphology, food habits, social organization and anti-predatory strategy. Further, because animal-environment relationships are a dynamic process and in view of the plasticity of animal behaviour, environment feedbacks play an important role in shaping habitat selection of an ungulate species.

5.1.2. Habitat selection in wapiti

Wapiti are found in a wide variety of environments, ranging from climax shrublands in Alaska (Batchelor 1965) to dry chaparrals in Arizona (Bryant and Maser 1982) to rainy forests in California (Harper et al. 1967). Regional, yearly and seasonal differences (Houston 1982), and sex related differences (Peek and Lovaas 1968, Flook 1970, Franklin and Lieb 1979) in habitat use are known. An apparent preference for the transition zone (ecotone) between forest and nonforest communities, related to the closeness of hiding cover and to the abundance of a rich and diverse forage species composition (edge effect) has also been noted (Skovlin 1982).

From these findings, stems the current definition of wapiti as an ecotone species (Geist 1982, Skovlin 1982), and as such it is "expected" to be highly opportunistic (Geist 1982) and to exibit flexibility in habitat selection (Gates and Hudson 1981). However, what characterizes an ecotone species is its adaptation to, and dependency upon, the biotic and physical features of transition zones between different habitats (Allee et al. 1949). In contrast, wapiti ~~are~~ creatures of forests, transitional zones, and open meadows. In some regions, wapiti use every vegetation type present (Houston 1982), in others habitat selection reflects seasonal habitat availability (Marcum 1975, Lenner 1977). Whereas in some regions the species is associated with a high level of habitat diversity, in others it uses extensive and well-defined vegetational units for specific activities.

The diverse habitat use patterns indicate opportunistic behaviour, and flexibility in habitat selection. Instead of a specialized adaptation to the limited ecotone environment, these characteristics are typical of ecological generalists. They suggest evolution in, and adaptation to, unoccupied, temporally hetereogeneous environments (Levins 1968), such as postglacial northern biomes (Geist 1982).

Several attempts to identify specific determinants of habitat selection have been made. Forage availability (Franklin et al. 1975) and/or quality (Hanley 1982), weather conditions (Beall 1974), presence and distance from escape cover, and human activities (Ward et al. 1973, Morgantini and Hudson 1979), have all been reported. However, interactions between biotic and physical environmental features, individual differences, and the ability of wapiti to adjust to local conditions, have impeded the identification of clear cause-effect relationships.

This study does not assess the relative importance of environmental determinants of habitat selection by wapiti as attempted by numerous authors (Beall 1974, Leege and Hickey 1977, Gates and Hudson 1981). In view of the large number of potential biotic and physical environmental features, such a study in the Panther-Red Deer-Clearwater region would have provided only site-specific knowledge without furthering our understanding of the evolutionary significance of habitat selection. Instead, I have chosen to describe seasonal and sex-related habitat selection patterns in the study region in an attempt to assess whether they can be interpreted as adaptations to northern environments.

5.2. Methods

5.2.1. Habitat classification

Habitat classification was based on vegetation structure and plant composition. Following field reconnaisance of the area, a tentative vegetation classification was developed based on gross species composition. The classification was continuously refined throughout the study period and compared to the detailed plant community classification of the region found in Holland and Coen (1982).

Vegetation communities were grouped in 12 broad habitat types (vegetation types, Table 5.1). To assess whether herd size depended upon the type of cover available (Dasmann and Taber 1956), the twelve habitat types were further grouped in three categories: forests, shrublands and open meadows.

5.2.2. Habitat selection

The study was based on continuous observations of wapiti

Table 5.1. The 12 major habitat types identified in the study area

	Habitat type	Ecoregion	Elevation	Repr.veg. types*
1	Alpine tundra	Alpine	2,300-2,500	L4,L5,L7,H1,H2
2	Krummholz	Upper subalp.-alpine	2,000-2,300	O19
3	Shrubland	Upper subalpine	2,000-2,300	S4,S8
4	Avalanche slopes	Lower-upp. subalp.	1,900-2,100	S2,S10
5	Open forests	Upper subalpine	1,900-2,200	O14,O18
6	Grassland slopes	Lower-upp. subalp.	1,600-2,000	H5,H14
7	Spruce forests	Montane-lower-upper subalpine	1,500-2,000	C37,O3,O17
8	Pine forests	Montane-lower-upper subalpine	1,500-1,900	C6,C18,C19
9	Deciduous forests	Mont.-lower subalp.	1,500-1,650	C16,C17,C22
10	Riverine habitats	Mont.-lower subalp.	1,500-1,700	C32,O6,S1,S3
11	Shrublands	Mont.-lower subalp.	1,500-1,750	S1,S3,S9,S10
12	Grasslands	Mont.-lower subalp.	1,500-1,650	——

* Representative vegetation types from the classification by Holland and Coen 1982

movements and distribution between December 1976 and November 1979.

Every month, fifteen days were spent in the field. Field work consisted of locating individual animals or herds, and of recording their movements and habitat selection for as long as possible. When wapiti went into forests, observations were continued from high vantage points, on surrounding hills or mountain ridges.

Monitoring habitat selection was restricted to day-light hours. However, observation of the same individuals sometimes extended over several days, when the same animals were located again the following morning. Physical characteristics, the presence of collared animals (Chapter 3), or herd structure helped in identifying individuals and herds.

The field technique adopted to assess habitat selection significantly reduces the otherwise common bias of observing more animals in open habitats only because that is where they are more visible.

5.3. Results

During the study, 605 observations were recorded, a cumulative total number of 14,758 animals were counted.

5.3.1. Habitat use

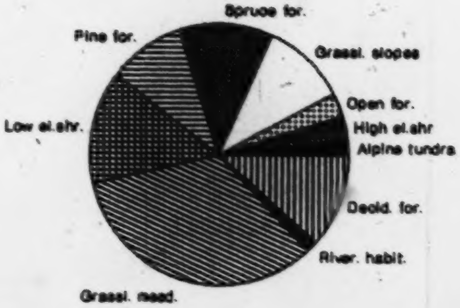
Wapiti used to some extent all the habitat types present in the region. However, a clear seasonal habitat use pattern is evident (Figure 5.1).

In winter, wapiti were mostly found in open grassland meadows (33.3%) along major river valleys. Coniferous and deciduous forests, and low elevation shrublands, were largely used for cover in areas of high human activity (Morgantini and Hudson 1979), or for escape. Observations on high elevation ranges were recorded during the winter hunting seasons (1976-77; 1977-78), when large herds of cows, yearlings and calves were chased onto alpine ranges immediately above grassland ranges along the Red Deer River. Use of south- and south-west facing grassland slopes was frequently observed along the Clearwater and Panther Rivers, but it was rarely detected within the Red Deer River region.

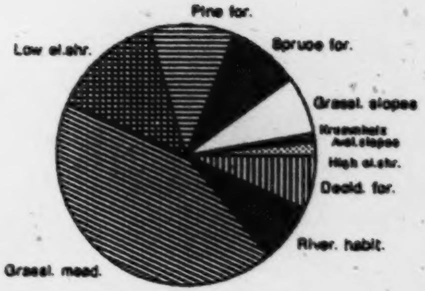
In spring, wapiti were found on intermediate ranges in Banff National Park (Chapter 3). During this season, habitat selection was remarkably similar to that observed in winter. The use of grassland meadows increased from 33.3 to 42.5 %, while a small decrease was observed in the use of forested habitats. Calving occurred throughout the region and specific calving grounds or preferred habitats for calving were not detected.

In summer, a major shift to high elevation ranges was observed. Alpine tundra, krummholz, and high elevation shrublands received the most use, but wapiti were also

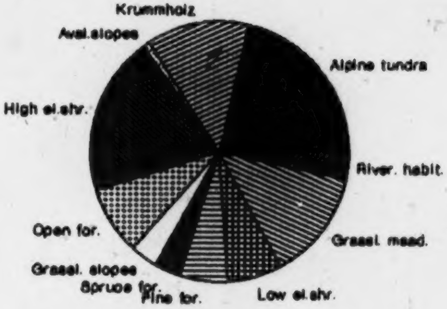
FIGURE 5.1. Seasonal habitat selection of wapiti (all sexes), based on the distribution of group observations, in the Red Deer-Panther-Clearwater region along the east slopes of the Rocky Mountains (1977-1979).



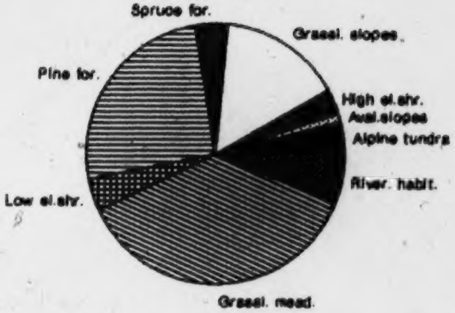
WINTER
(207)



SPRING
(179)



SUMMER
(117)



FALL
(88)

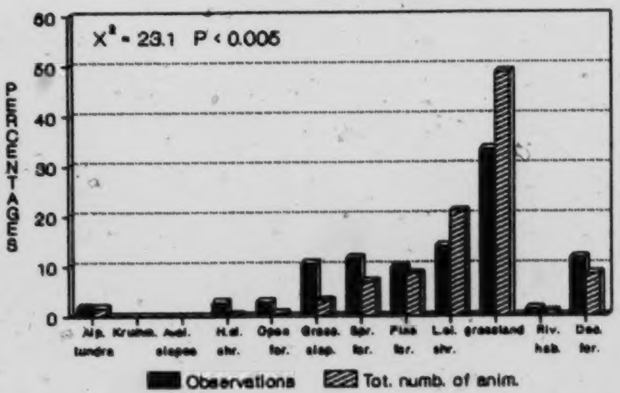
observed in forested habitats and low elevation grasslands.

During fall, habitat selection was not only determined by migratory movements onto lower elevations and changes in weather patterns (Chapter 3), but also by the social behaviour associated with the rut. Wapiti were found in small herds (harems) of 5-15 animals, whose distribution and movements were often affected by the harem bull. The use of grassland slopes, in the upper and lower subalpine ecoregions, was extensive. Pine forests and low elevation grasslands also received heavy use. Wapiti frequently occurred in areas with a high vegetational hetereogeneity, i.e. a mosaic of small stands of open or dense pine and spruce forests, patches of shrubland and sedge/grass meadows, generally associated with small creeks and poorly drained sites.

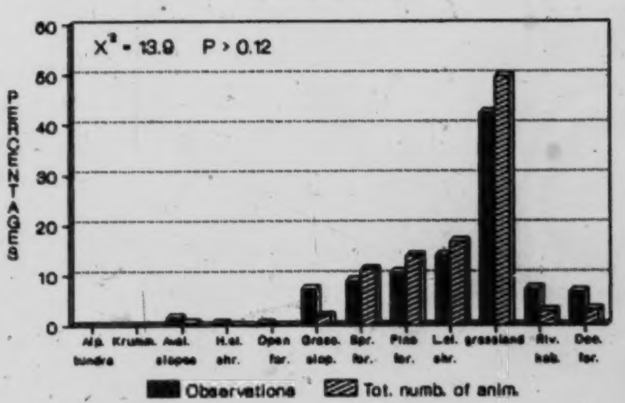
The use of percentage group (herd) observations to assess habitat use of a gregarious species such as the wapiti can be misleading. It shows, for instance, that in the summer low elevation grasslands (13.7%), and alpine and upper subalpine ranges (19.7%, 12.8%, 21.4%) are of similar importance to the animals in the region. Yet, when habitat use is assessed on the basis of the total number of animals counted, the percentage use of low elevation grasslands drops to 9.7% (140 animals) (Figure 5.2). Conversely, the use of high elevation ranges (habitats #1,2,4) increased from 53.9 % to 72.4 % (1079 animals), clearly indicating the importance of alpine ranges

FIGURE 5.2. Habitat selection of wapiti (all sexes) in the Red Deer-Panther-Clearwater region along the east slopes of the Rocky Mountains. A comparison between seasonal habitat selection based on the distribution of group observations and habitat selection based on the total number of animals counted (1977-1979).

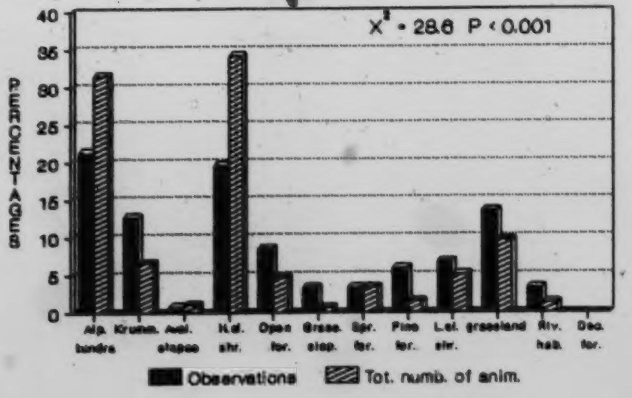
WINTER (December-April)



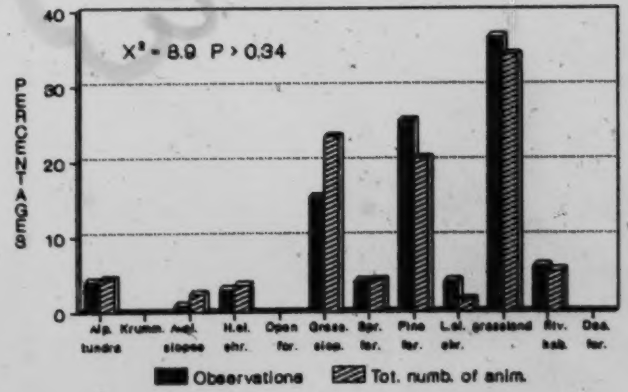
SPRING (May-June)



SUMMER (July-August)



FALL (September-November)



to the summer ecology of wapiti.

A similar difference between percentage distribution of group and of individuals was found in the other seasons (Figure 5.2). However, it was not as marked as in the summer because of differences in variations of herd sizes.

5.3.2. Herd size

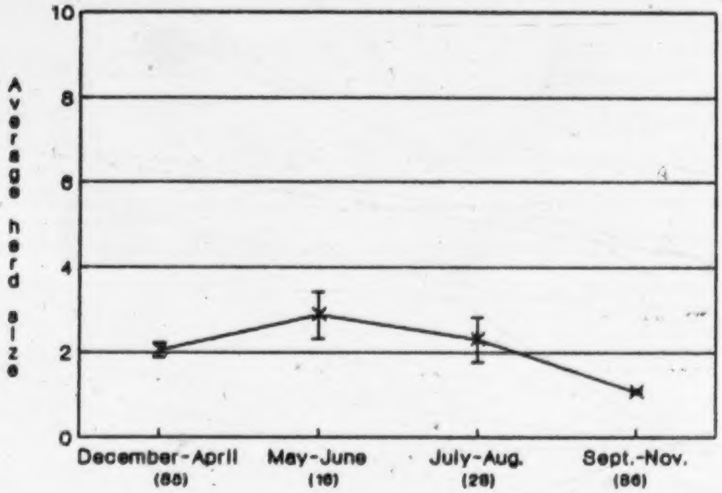
The difference in habitat use distribution between percentage group observations and percentage of total number of animals counted reflected large variations in herd size.

A significant difference ($P<0.001$) was found in herd size, both between the sexes and among seasons (Figure 5.3, Table 5.2). Overall, males were found in much smaller herds than females (cows-calves-yearlings), averaging 1.9 animals vs. 30.2 animals per observation.

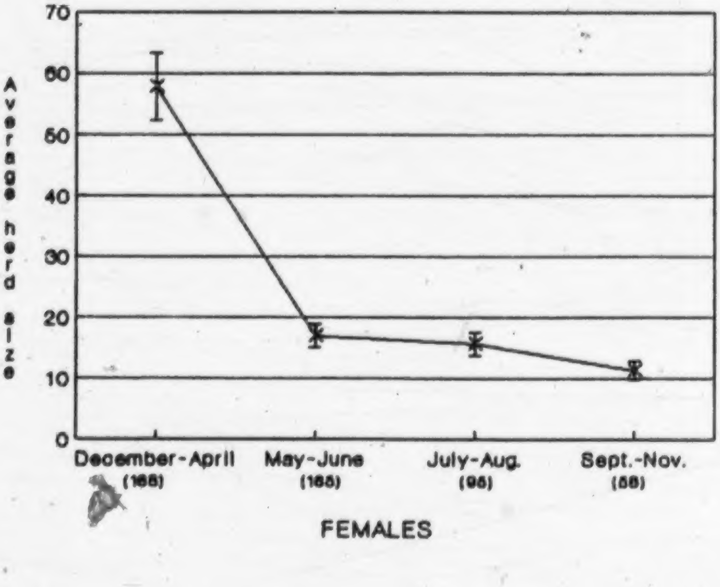
Seasonal differences among males were due to significantly larger herd sizes in spring than in fall and winter ($P<0.05$), and to smaller herd sizes in the fall than in any other season ($P<0.05$). However, within each season, no statistically significant difference in herd size among the twelve habitats types, and the three habitat categories, was found (Appendix C).

Female herds were largest in winter ($\bar{x}$ = 57.8), but not significantly different among the other seasons. Average herd size among the twelve habitat types was significantly different in winter and summer, but not in spring and fall

FIGURE 5.3. Herd sizes of male and female wapiti herds in the Red Deer-Panther-Clearwater region along the east slopes of the Rocky Mountains (1977-1979).



MALES



FEMALES

J

Table 5.2. Seasonal herd sizes in males and females wapiti in the Red Deer-Panther-Clearwater region. (1977-1979).

ANOVA

Source of variation	SS	df	MS	F-ratio	Sig. level
MAIN EFFECTS	2322646.34	4	58161.58	35.252	0.0000
Sex	62572.92	1	62572.92	37.926	0.0000
Season	160971.18	3	53657.06	32.522	0.0000
2-FACTOR INTERACTIONS					
sex:season	35921.84	3	11973.95	7.258	0.0001
RESIDUAL	970118.86	588	1649.86		
TOTAL (CORR.)	1238687.0	595			

Table of average herd sizes

	n	Average	St. Err.
ALL SEASONS			
Males	110	1.91a	.16
Females	486	30.17b	2.22
ALL SEXES			
Winter	203	48.16a	4.73
Spring	181	15.77b	1.78
Summer	118	13.12bc	1.61
Fall	94	7.40c	1.08
SEX BY SEASON			
Males:winter	35	2.06a	.18
Males:spring	16	2.87b	.54
Males:summer	23	2.30ab	.52
Males:fall	36	1.08c	.04
Females:winter	168	57.77d	5.44
Females:spring	165	17.01e	1.92
Females:summer	95	15.74e	1.90
Females:fall	58	11.33e	1.55

Within level of classification, values followed by different letters are significantly different at $P<0.05$

(Appendix C). No clear relation of summer herd size to habitat was detected, since no difference was found among habitat categories. However, female herd sizes in winter were significantly ($P<0.02$) larger in shrublands ($\bar{x}$ = 85.4), smaller in forests ($\bar{x}$ = 39.7) and of intermediate sizes in grasslands ($\bar{x}$ = 62.2).

5.3.3. Sex segregation

In view of the difference in herd sizes between males and females, habitat distribution is compared on the basis of percentage of total number of animals counted (Figure 5.4).

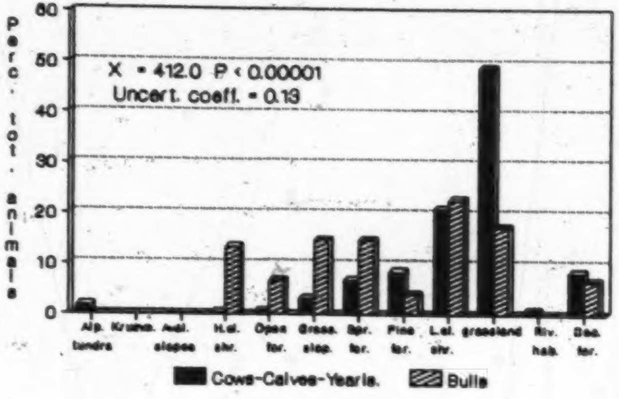
A significant difference in habitat selection between the sexes was found for every season.

In winter, bulls were observed mostly as single individuals or in small herds of two or three animals. They were found with the same frequency in all the habitats used. Bulls occurred on the periphery of winter ranges used by large herds of cows, calves and yearlings, usually further west, on more rugged terrain. Their habitat use in winter largely reflected this wide distribution.

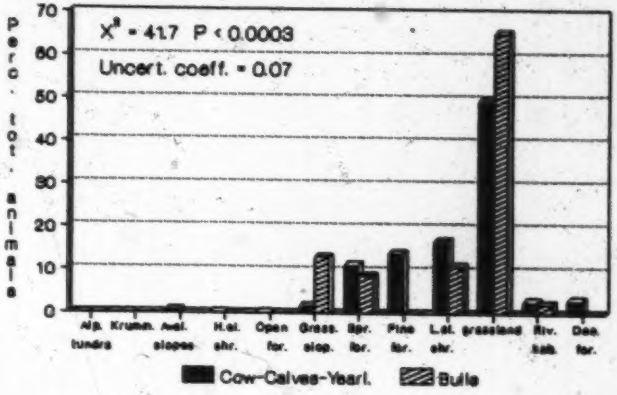
Outside Banff National Park, bulls were observed in coniferous and deciduous forests surrounding the Ya Ha Tinda Ranch and the Corners, on the west end of Ribbon Flats and along DogRib Creek. Within the boundary of Banff National Park, the meadows, shrublands and coniferous forests in the divide area between the Panther and the Red Deer River

FIGURE 5.4. Seasonal habitat selection (individual observations) of bulls and cow-calf-yearling herds in the Red Deer-Panther-Clearwater region along the east slopes of the Rocky Mountains. (1977-1979).

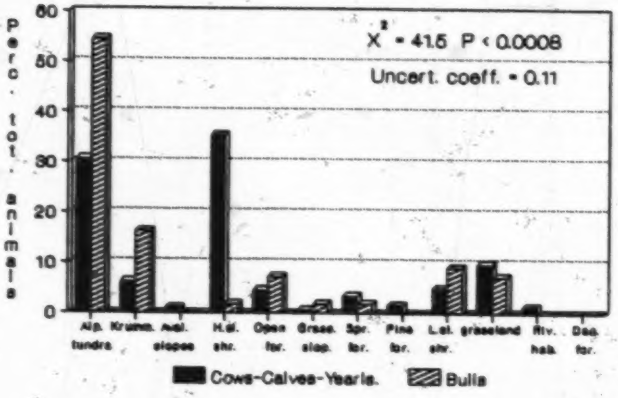
WINTER (December-April)



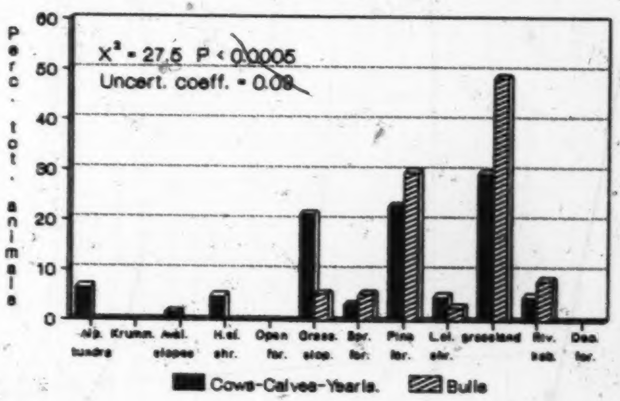
SPRING (May-June)



SUMMER (July-August)



FALL (September-November)



drainages received so frequent use that this area was considered the only clearly identifiable bull winter range in the region.

In winter, cow-calf-yearling herds were mostly found in open grasslands. Shrublands and forests were mostly used during midday as cover (see Morgantini and Hudson 1979).

In spring, cow-calf-yearling herds showed only a marginal change in habitat selection ($P>0.05$). Conversely, a significant increase in the use of open grasslands by bulls (17% in winter vs 65% in spring, $t=5.46$, $P<0.0005$), and an overall decrease in the use of forested habitats, were detected.

A major change in habitat selection by bulls and cows-calves-yearlings was observed in the summer. This coincided with a regional and topographical change in distribution (Chapter 3).

During summer, all nursery herds were found on alpine and upper-subalpine ranges, while the use of all the other habitats was mostly restricted to small groups of bulls, barren cows and yearlings. In this season, 35 % of all cow-calf-yearling observations were recorded in upper subalpine shrublands, mostly along valley floors, benchlands and cirque basins. Thirty percent were observed on open alpine tundra, while about 6 % in open, stunted Engelmann spruce forests (Krummholz) on the boundary of alpine tundra. Similarly, bulls were found on alpine tundra, in Krummholz, and in the open forests in the upper subalpine. However, bulls were not observed in high elevation shrublands.

During fall, because of the rutting season, the distinction between habitat selection by bulls and by cows-calves-yearlings is questionable. In September and part of October, one mature bull was always present in cow-calf herds and, frequently, subdominant and younger bulls ranged within 100-200 m from the harem herd. In the later part of October, younger bulls were still rutting. Nonetheless, a sex differential in habitat selection between September and November was still evident. Cow-calf-yearling herds (harem herds) extensively used grassland slopes, pine forests and low elevation grasslands, while individual bulls were frequently seen in pine forests and low elevation grasslands.

5.4. Discussion

5.4.1. Habitat selection

In the Panther-Red Deer-Clearwater region, wapiti of both sexes were commonly found in grassland habitats, on alpine tundra or in surrounding shrubland meadows. It can be suggested that this habitat use pattern is biased because of the methods used in locating animals. Clearly there is a higher chance of observing wapiti in open habitats. While the bias, inherent in field studies based on animal observations, was partially addressed by the field technique (5.2.2), it may still be present. However, heavy use of grassland meadows in winter, spring and fall is also indicated by the diet composition of wapiti in the region (Chapter 4). During these seasons, the diet consisted largely of rough fescue, a species which, in this region, is found primarily in grassland meadows (Morgantini and Russell 1983). When wapiti were disturbed from open habitats, in addition to a shift in habitat use (Morgantini and Hudson 1979), a change in diet was also observed (Morgantini and Hudson 1985). In summer, wapiti forage was also commonly found on alpine tundra and high elevation shrublands (Chapter 4).

Habitat use patterns observed in this study may reflect habitat availability and not habitat preference. The use of open grasslands in winter, spring and fall may indeed reflect greater availability. Nonetheless, wapiti did feed in grasslands and that is where the highest quality forage is available. This may be chance or an indication of preference.

Wapiti are believed to prefer open country habitats and grasslike vegetation. Some authors, however, refer to them as an "ecotone species", utilizing the transitional zone between forests and grasslands (Skovlin 1982). Within the study region wapiti did not behave as an ecotone species. In winter, spring and fall, wapiti did use well defined vegetation types. This may reflect the relatively simple vegetational structure of the study region (Morgantini 1979, Morgantini and Russell 1983), with well defined boundaries between grassland, forest and shrubland communities. And even though, in terms of plant species composition, a transitional zone between vegetational communities can be found, these zones are too small in size to be of ecological significance to a highly mobile and gregarious species. Wapiti were frequently observed feeding, and sometimes resting, in the middle of large extentions of grasslands. Frequently, forest and shrubland communities provided hiding cover (Morgantini and Hudson 1979, 1985). Wapiti used the transition zone between these communities when going from one habitat to another, and were consistently observed to move away from the edge of open habitats.

During summer, wapiti were observed widely spread out over large expanses of alpine tundra. This habitat type is characterized by a highly diverse mosaic of plant communities (Holland and Coen 1982). However, in view of the uniform composition of summer diet (Chapter 5), it is questionable whether vegetational diversity of the herb layer is the factor determining wapiti use.

In conclusion, the selection of habitats in the Panther-Red Deer-Clearwater region is consistent with our knowledge of wapiti behavioural and physiological requirements. Because of the species' large body size, habitat selection is expected to be determined more by forage constraints than by the thermal environment (Bell 1971, Gates and Hudson 1981). However, the availability of escape and hiding cover may override foraging requirements. In this study, the use of grassland meadows and summer habitats appears to reflect availability and quality of forage resource. The use of forests and shrublands seems to be largely related to the need for escape cover. It is within these overall requirements that wapiti may adjust to other environmental factors such as insect harassment and water availability in summer, weather conditions, and inter- and intra-specific interactions.

5.4.2. Sex differences in gregariousness

The evolution of gregariousness has been explained as an antipredatory strategy suited to open areas (Hamilton 1971, Jarman 1974).

In cervids, gregariousness is considered an adaptive strategy, available to individuals to best respond to local environmental factors. Variations in herd sizes have been related to the degree of cover (Dasmann and Taber 1956, Peek et al. 1974) and the distribution of forage (Clutton-Brock *et al*. 1982). With regard to wapiti, Gates (1980) suggested that gregariousness may be seen as a feeding strategy to maximize energy intake in periods of limited forage availability and quality In large groups, wapiti may be able to spend more time feeding and less in watching out for predators. However, animals must disperse when forage supplies are low. Hanley (1982) noted that, between May and October, average group size in wapiti decreased with decreasing forage quality and availability.

It is well known that mature adult males of ungulates tend to be solitary, while females tend to be more gregarious (Leuthold 1977). If each sex were considered a different species (Trivers 1972, Clutton-Brock *et al*. 1982), the male "species" would be defined as solitary, while the females "species" would be defined as gregarious. This suggests a strong sexual dimorphism, each sex having evolved different behavioural adaptations to the same environment. Sexual dimorphism can be seen as another aspect of species polymorphism, where "natural selection diversifies the gene pool in such a way that two... genotypes having optimal adaptiveness in different subenvironments are produced" (Dobzansky *et al*. 1977: 117). In this context, the degree of gregariousness could be considered a sex-linked adaptation. This is consistent with Geist's hypothesis that larger herd sizes in females are linked to the safety of their offsprings (Geist 1982). Differently, reproductive success of males depends on large body size. Hence, male wapiti "ought" to maximize body size by exploiting small habitat patches with high quality forage (Geist 1982). However, the question remains as to whether the adaptation is a response to seasonal environments.

In this study, the sex difference in average herd size was consistent with the expected sexual dimorphism. Bull herds were always small, consisting mostly of single-individuals, whereas female herds were consistently larger. However, analysis of habitat preferences indicated no significant difference in herd size, both in males and females, between different habitats in all seasons. The only exception, i.e. a larger congregation of cows in shrublands in the winter, can be attributed to the configuration of the winter range, where wapiti tended to concentrate in shrublands at dawn and dusk on their movements from or to open grasslands (Morgantini and Hudson 1979). This suggests that environmental influences may be secondary determinants of gregariousness. Therefore, I suggest that gregariousness in wapiti may not be an adaptation to environmental factors, such as predators and forage availability, but it may be directly related to reproductive behaviour.

The reproductive behaviour of wapiti males involves intense fighting between competing individuals. During the rutting season, mature bulls are found as individuals, either isolated, or with a female harem herd. The encounter of two males results in a fight, or in energy demanding advertisement displays (Clutton-Brock et al. 1979). After the rut, males in the closely-related red deer still show a lingering libido and show copulatory behavior and aggressive threats toward rival males (Lincoln _et al_. 1970). Similarly, male wapiti continue to display a high level of dominance behaviour (Franklin and Lieb 1979).

Behaviour during the rut is extremely important to reproductive success. For male wapiti to aggregate following an active fighting season would require a radical change in behaviour patterns. Since learning and traditional behaviour are important components of wapiti behavioural make-up, it can be speculated that the formation of male herds could be achieved only at the expense of individual behavioural characteristics that are essential to reproductive success.

On the other hand, female wapiti are herded during the rutting season. Strong individualistic tendencies would rapidly disperse the harem herd, since one lone bull could not keep the herd together and, at the same time, being involved in intrasex dominance behaviour. Thus, wapiti females show gregarious traits at a very essential time in their reproductive life. For females, it is important to remain in the harem, so that their male offsprings may share the genes of the strongest males, and, with that, have better chances of successful reproduction. Hence, it seems reasonable that females' tendency to herd together, so important during the rutting season, should be maintained at all other times, if it is not otherwise negative for survival and offspring rearing.

The hypothesis presented here suggests that the gregarious habits of both male and female wapiti are essentially a carry-over of the all-important reproductive behaviour into non-reproductive seasons. Additional concurring benefits, such as lower predation and better resource exploitation, may have played a role in the development of the sex-linked adaptation, namely the gregarious habit. Within each sex, the degree of gregariousness of individual animals may represent an adaptive strategy to the local environment.

As stated elsewhere, it is not appropriate to make generalizations on wapiti adaptive behaviour. Male herds larger than those observed in the Panther-Red Deer-Clearwater region have been historically reported and do occur in areas with high population densities. Nonetheless, typically, male herds are still smaller than female herds (Houston 1982).

5.4.3. Sex segregation in habitat selection

This study found a clear difference in habitat use between male and female wapiti. These results are consistent with our knowledge of distribution and habitat selection of male and female herds of wapiti and red deer (Franklin and Lieb 1979, Clutton-Brock et al. 1982). However, this study also showed that the sex differential in habitat use was not related to differences in herd size.

Several authors have discussed the ecological and adaptive significance of sex segregation in northern ungulates (Morgantini and Hudson 1981, Clutton-Brock et al. 1982, Jakimchuk et al. 1987). Four major hypotheses have been developed, and are identified below here with the name of the authors who proposed them.

5.4.3.1. Shank hypothesis

In the first hypothesis, ecological separation between the sexes is thought to reflect differences in body size and, therefore, different behavioural patterns and habitat requirements. This hypothesis, which Shank (1979) extensively discussed for bighorn sheep, has been applied by Geist (1982) to wapiti. In order to increase reproductive fitness, female wapiti 'ought' to maximize security (anti-predatory strategies) at the cost of low quality forage, while males 'ought' to maximize body growth by foraging on highly nutritious forage found in widely dispersed small patches of habitat.

The hypothesis seems based on three assumptions: a) male wapiti select for higher quality forage; b) higher quality forage is found only in habitat pockets and not in habitats used by large female herds; c) males and females select for different habitats. These assumptions are not consistent with the results of this study and with our knowledge of wapiti and red deer foraging behaviour. For instance, according to this hypothesis, after the rut and throughout the winter, exhausted males are expected to search for pockets of high quality forage, while females will compromise forage quality for security in large herds in open habitats. However, there is evidence indicating that males in the closely-related red deer are on a poorer winter quality diet than females, and that they compensate through higher forage intakes (Staines _et_ _al_. 1982, Clutton-Brock _et_ _al_. 1982). The different diet was explained in terms of spatial distribution. Flook (1970) observed that male wapiti had a greater degree of tooth wear than females, possibly indicating higher intakes or more coarse, hence less digestible (Van Soest 1982) forage. Wapiti forage quality studies in the Panther-Red Deer-Clearwater region show that grass species growing in the open grassland habitats used by large herds of females are of significantly better quality than species growing in other habitats (Morgantini and Russell 1983, Morgantini and Hudson 1985). It follows that males, by avoiding open grasslands, are likely feeding on poorer forage than females. However, due to their larger rumen size, adult males may be more efficient in using forage of higher fiber content that would have a lower digestibility value in smaller bodied animals (cows and calves). With regard to habitat selection, Shank's hypothesis assumes that males and females select for _different_ habitat. However, several studies have failed to report a clear-cut difference in habitat selection between the sexes (Franklin and Lieb 1979). Within the Panther-Red Deer-Clearwater region, the results of this study showed no consistent geographical separation between the two sexes. Males were repeatedly observed in areas occupied at an earlier or later date by females. Hence, sex segregation involved only the degree of utilization of the same habitats. This was especially evident in spring when a significant increase in the use of open grasslands by males was observed. However, these males never joined the already present female herds. Finally, the wide range of male habitat selection patterns throughout the continent (Skovlin 1982) indicates that males are not restricted to a limited set of habitat requirements as Shank's hypothesis implies.

5.4.3.2. Geist-Bromely hypothesis

The second hypothesis suggests that the segregation of males from females has evolved as a male anti-predatory strategy. Males, exhausted by the breeding season and easily distinguishable from females, would be subjected to selective predation during winters unless they disperse and avoid female herds where they could be easily singled out (Geist and Bromley 1978, Geist 1982). However, gregariousness is recognized as a powerful protection against predation (Hamilton 1971). Therefore, the advantage of solitarity versus gregariousness, regardless of conspicuousness of the animals, is questionable. In reality, younger males (1-3 year old), although as easily identifiable by predators as older males, are found in female herds. In addition, this hypothesis by itself cannot explain the maintenance of sex segregation in spring and early summer, when antlers are either missing or small.

5.4.3.3. Geist-Petocz hypothesis

The third hypothesis suggests that males avoid females in winter to minimize intraspecific competition with their offspring (Geist 1982). In order to maximize reproductive fitness, "...males ought not to compete with their offspring during ontogeny, nor with the prospective mothers of their offspring" (Geist and Petocz 1977). The hypothesis implies the presence of sex-linked (Wickler 1977) altruistic behaviour. To not "compete" with females, males would risk reducing their own reproductive potential by using alternative, possibly suboptimal habitats.

Again, this hypothesis is not consistent with our understanding of wapiti behaviour. In periods of severe winters, female wapiti are known to displace their own offspring for access to limited resources. Consequent deterioration of body condition of the calves and high mortality has been reported (Houston 1982). Since females would compete with their offspring for forage, it is difficult to imagine such altruistic behaviour in males, that have so much less reproductive investment in any one offspring.

Finally, the existence and importance of kin selection is still a subject of great doubt and debate.

5.4.3.4. Morgantini-Hudson hypothesis

The fourth hypothesis was proposed by Morgantini and Hudson (1981) to explain the evolution of sex segregation in bighorn sheep. The hypothesis, as applied to wapiti, assumes that the occurrence of mature males with females in mixed herds would cause a higher frequency and intensity of sexual, agonistic, herding, and dominance behaviours at times when reproduction is not possible. Hence, to minimize energy expenditures associated with sexually-related social interactions, the coexistence of mature males with females in periods other than the breeding season was selected against despite the risk for any one sex to feed on poorer quality forage. The hypothesis is consistent with the results of this study and with our understanding of reproductive physiology and behaviour of red deer (Lincoln et al. 1970) and wapiti (Franklin and Lieb 1979, Houston 1982). This hypothesis does not invoke, directly or indirectly, altruistic behaviour or kin selection because it considers habitat and spatial segregation as evolved to maximize male individual fitness. Further, it does not assume any fixed, predetermined animal-environment relationship (forage quality and availability, habitat-herd sizes, antipredatory strategy, etc). It allows for physiological and/or behavioural species-specific or individual requirements to shape habitat preferences on the basis of local environmental conditions. In this view, minimization of intraspecific competition, predator avoidance or sexual-dimorphism related niche differences could be all seen as by-products of the avoidance by males of sexual agonistic stimuli outside the rutting season.

5.5. Conclusions

Patterns of habitat selection in the study region appear to reflect local vegetational structure, forage availability and quality, and availability of hiding cover. In this context, no species-specific adaptation to seasonal environments can be found, beside the basic imperative of any ungulate to feed and to avoid being fed upon, within local environmental conditions and physiological constraints.

Sex-related differences in herd sizes and habitat utilization also may not reflect any specific adaptation to changing environments. Instead, they may represent behavioural patterns evolved in association with the reproductive activities and behaviour of the species.

5.6. Literature cited

ALLEE, W. C., A. E. EMERSON, O. PARK, and K. P. SCHMIDT. 1949. Principles of animal ecology. W.B. Saunders Company, Philadelphia and London. 837pp.

ANDERSON, L. T. 1973. An analysis of habitat preference in mice as a function of prior preference. Behavior 47: 302-339.

ARNOLD, G. W. 1964. Factors within plant associations affecting the behavior and performance of grazing animals. in D. J. Crisp (Ed.), Grazing in terrestrial and marine environments. Blackwell Sci. Publ., Oxford. 407pp.

BELL, R. H. V. 1971. A grazing ecosystem in the Serengeti. Sci. Am. 225: 86-93.

BEALL, R. C. 1974. Winter habitat selection and use by a western Montana elk herd. Ph. D. Thesis, Univ. Montana, Missoula. 197pp.

BROWN, J. L. and G. H. ORIANS. 1970. Spacing patterns in mobile animals. Ann. Rev. Ecol. Syst. 1:239-262.

CLUTTON-BROCK, T. H., S. D. ALBON, R. M. GIBSON, and F. E. GUINNESS. 1979. The logical stag: adaptive aspects of fighting in red deer (Cervus elaphus L.). Anim. Behav. 27:211-225.

CLUTTON-BROCK, T. H., F. E. GUINNESS, and S. D. ALBON. 1982. Red deer. Behavior and ecology of two sexes. Univ. Chicago Press, Chicago. 378pp.

DOBZHANSKY, T., F. J. AYALA, G. L. STEBBINGS and J. W. VALENTINE. 1977. Evolution. W.H. Freeman and Co. San Francisco. 572pp.

DASMANN, R. F., and R. D. TABER. 1956. Behavior of Columbian black-tailed deer with reference to population ecology. J. Mammal. 37: 143-164.

EISENBERG, J. F., and M. LOCKART 1972. An ecological reconnaissance of Wilpattu National Park, Ceylon. Smithsonian Contr. Zool. 101. Smithsonian Inst., Washington.

FLOOK, D. R. 1970. A study of sex differential in the survival of wapiti. Can. Wildl. Serv. Rep. Ser. No. 11. Queens Printer, Ottawa. 71pp.

FRANKLIN, W. L., A. S. MOSSMAN, and M. DOLE. 1975. Social organization and home range of Roosevelt elk. J. Mammal. 56: 102-118.

FRANKLIN, W. L., and J. W. LIEB. 1979. The social organization of a sedentary population of North American elk: a model for understanding other populations. Pages 185-195 in M. S. Boyce and L. D. Hayden-Wing (Eds.), North american elk: ecology, behavior and management. Univ. Wyoming Press, Laramie.

GATES, C. C. 1980. Patterns of behaviour and performance of wapiti (Cervus elaphus nelsoni) in the boreal mixed wood forest. Ph. D. Thesis. Univ. Alberta, Edmonton. 240pp.

GATES, C. C. and R. J. HUDSON. 1981. Habitat selection by wapiti in a boreal forest enclosure. Naturaliste Can. 108: 153-166.

GEIST, V. 1971. A behavioural approach to the management of wild ungulates. Pages 413-424 in E. Duffy and A. S. Watt (Eds.), The scientific management of animal and plant communities for conservation. 11th Symp. British Ecol. Soc., Blackwell Sci. Publ., Oxford.

GEIST, V. 1982. Behavioral Adaptive Strategies. Pages 219-278 in J. W. Thomas and D. E. Toweill (Eds.), Elk of North America. Ecology and management. Stackpole Books, Harrisburg, Pa. 698pp.

GEIST, V. and R. G. BROMLEY. 1978. Why deer shed antlers. Zeitschrift fur Saugetierkunde 43: 223-231.

GEIST, V., and R. G. PETOCZ. 1977. Bighorn sheep in winter: do rams maximize reproductive fitness by spatial and habitat segregation from ewes? Can. J. Zool. 55: 1802-1810.

HAMILTON, W. D. 1971. Geometry for the selfish herd. J. Theor. Biol. 31: 295-311.

HANLEY, T. A. 1982. Cervid activity patterns in relation to foraging constraints: western Washington. Northw. Sci. 56: 208-217.

HOLLAND, W. D. and G. M. COEN. 1982. Ecological (biophysical) land classification of Banff and Jasper National Parks. Vol. II: Soil and vegetation resources. Alberta Inst. of Pedology. Publ. No. SS-82-44. 540pp.

HOUSTON, D. B. 1982. The Northern Yellowstone elk. Ecology and management. Macmillan, New York. 474pp.

JARMAN, P. J. 1974. The social organization of antelope in relation to their ecology. Behavior 48: 215-267.

JAKIMCHUK, R. D., S. H. FERGUSON, and L. G. SOPUCK. 1987. Differential habitat use and sexual segregation in the central arctic caribou herd. Can. J. Zool. 65: 534-541.

LEEGE, T. A., and W. O. Hickey. 1977. Elk-snow habitat relationships in the Pete King Drainage, Idaho. Wildl. Bull. No. 6, Idaho Dept. Fish Game, 23pp.

LEUTHOLD, W. 1977. African ungulates. A comparative review of their ethology and behavioral ecology. Springer-Verlag, New York. 307pp.

LEVINS, R. 1968. Evolution in changing environments. Princeton Univ. Press, Princeton, N.J. 120pp.

LINCOLN, G. A., R. W. YOUNGSON, and R. V. SHORT. 1970. The social and sexual behaviour of the red deer stag. J. Reprod. Fert., Suppl. 11: 71-103.

LONNER, T. N. 1977. Long Tom Creek Study. Pages 25-68 in Ann. Prog. Rep., Mont. Coop. Elk/logging study, Bozeman, Montana.

MORGANTINI, L. E. 1979. Habitat selection and resource division among bighorn sheep, elk and mule deer in western Alberta. M.Sc. Thesis. Univ. Alberta. Edmonton. 187pp.

MORGANTINI, L. E., and R. J. HUDSON. 1979. Human disturbance and habitat selection in elk. Pages 132-139 in M. S. Boyce and L. D. Hayden-Wing, eds. North American elk: ecology, behavior, and management. Univ. Wyoming, Laramie.

MORGANTINI, L. E. and R. J. HUDSON. 1981. Sex differential in use of the physical environment by bighorn sheep (*Ovis canadensis*). Can. Field Nat. 95: 60-74.

MORGANTINI, L. E., and R. J. HUDSON. 1985. Changes in diets of wapiti during a hunting season. J. Range Manage. 38: 77-79.

MORGANTINI, L. E., and W. B. RUSSELL. 1983. An assessment of three selected elk winter ranges in the Rocky Mountains region. Unpubl. Rep. prepared for the Alberta Fish and Wildlife Division by Wildlife

Resources Consulting Ltd. Edmonton. Alberta Fish and Wildlife Files, Edmonton, Alberta. 265pp.

MARCUM, C. L. 1975. Summer-fall habitat selection and use by a western Montana elk herd. Ph. D. Thesis. Univ. Montana, Missoula. 188pp.

PEEK, J. M. and A. L. LOVAAS. 1968. Differential distribution of elk by sex and age in the Gallatin winter range, Montana. J. Wildl. Manage. 32:553-557.

PEEK, J. M., R. E. LeRESCHE, and D. R. STEVENS. 1974. Dynamics of moose aggregations in Alaska, Minnesota and Montana. J. Mammal. 55: 126-137.

SHANK, C. C. 1979. Sexual dimorphism in the ecological niche of wintering Rocky Mountain bighorn sheep. Ph. D. Thesis, Univ. Calgary, Calgary. 193pp.

SKOVLIN, J. M. 1982. Habitat requirements and evaluation. Pages 369-414 in J. W. Thomas and D. E. Toweill (Eds.), Elk of North America. Ecology and management. Stackpole Books, Harrisburg, Pa.

STAINES, B. W., J. M. CRISP and T. PARISH. 1982. Differences in the quality of food eaten by red deer (Cervus elaphus) stags and hinds in winter. J. Appl. Ecol. 19: 65-77.

TRIVERS, R. L. 1972. Parental investment and sexual selection. Pages 136-179 in B. Campbel (Ed.), Sexual selection and the descent of man. Aldine, Chicago.

VAN SOEST, P. J. 1982. Nutritional ecology of the ruminant. O & B Books, Inc., Corvallis, Oregon. 374pp.

WARD, A. L., J. J. CUPAL, G. A. GOODWIN, and H. D. MORRIS. 1973. Elk behavior in relation to cattle grazing, forest recreation, and traffic. Trans. N. Am. Wildl. Nat. Res. Conf. 38: 327-337.

WECKER, S.C. 1964. Habitat selection. Sci. Am. 211: 109-116.

WICKLER, W. 1977. Sex-linked altruism. Zeitschrift fur Tierpsychologie 43: 106-107.

6. SYNTHESIS

6.1. Overview

In this study, I have tried to assess whether behavioural patterns of wapiti, specifically migratory behaviour, forage selection, and habitat use, can be considered adaptations to the northern mountain environment. To do this, I have first looked at the most outstanding behaviour observed in the wapiti in the study area; namely seasonal migration. Without attempting to explore the origin of such behaviour, I have focussed on movement patterns, on respective locations of winter and summer ranges, and on the possible relationship between migration and the quality and availability of food on seasonal ranges. Finally, habitat use and selection has been examined, in relation to each seasonal range first, and then as an aspect of the social behaviour of wapiti in the region.

The results of this study often contradict the hypothesis that the observed behavioural patterns are adaptations. Although definite patterns of behaviour can be identified for this population, several exceptions were found.

During the last decade, there has been a considerable interest in the application of the optimality theory (Cody 1974) to the interpretation of activity patterns (McCleery 1978, Belovsky 1981, Owen-Smith and Novellie 1982, Pyke 1984, Davies and Houston 1984, Sibly and Calow 1986). The theory is based on the assumption that "... natural selection shape(s) the decision-making processes of animals in such a way that the resulting behaviour sequences are optimally adapted to the current environmental circumstances" (McFarland 1977). Decision-making will optimize behavioural patterns so as to maximize survival and reproductive success. However, the "optimization" scenario implies that each past behaviour and decision-making must also have been optimal, thus negating the necessity for further selection. In addition, limitations to the general applicability of the optimization theory to the real world have been recognized, such as individual variations and the stochastic nature of the environment (McFarland 1977), the complexity of alternative choices (Cody, 1974), and the simple fact that individuals can make mistakes (Festa-Bianchet 1987).

The migratory patterns observed during this study indicate that wapiti are not "optimal" strategists. If they were, they would be expected to obey "the law of least effort" that is "...necessary resources must be obtained with a minimum effort in order to maximize benefits derived" (Geist 1982). The long range travel of wapiti onto far away summer ranges, when ranges of similar quality forage are available and are already utilized by individuals from the same population, cannot be explained by the optimization theory. On the contrary, this study found that tradition was a major factor shaping the selection of seasonal ranges in the Red deer-Panther-Clearwater region, and that the overall migratory patterns may reflect the original dispersal of wapiti from their point of reintroduction.

With regard to forage selection, all herbivores living in northern environments had to evolve a basic feeding strategy dependent on seasonal changes in forage quality and availability. Species-specific differences can be related to differences in digestive physiology which may have been shaped by the biotic and physical environments in which they evolved. The search for and ingestion of highly nutritious forage in spring and summer are widespread adaptive traits in the northern environment. However, the fact that some wapiti forage on high quality forage on alpine ranges and some of them do not, indicates that in this species there may have been a selective advantage to a strategy which allows individuals to meet their own nutritional requirements depending on local environmental conditions. Wapiti differ from other species in their ability to adjust to different forage resources, due to their highly generalistic digestive physiology.

Patterns of habitat selection within the study region appear to reflect local vegetational structure, forage availability and quality, and availability of hiding cover. In this context, no unique adaptation to northern environments can be found, besides the basic imperative of any ungulate to feed, and to avoid being fed upon.

Additional analysis of habitat use, with respect to herd size and structure, has indicated significant sex differences in herd size, and a marked sex segregation. Two theories have been proposed to explain these differences. Both theories could be be extrapolated from the study population to the whole species.

With respect to herd size, the study showed that mature males, except when with the harem herd, are mostly solitary or in very small groups. On the other hand females, except for a few days when calving, are typically found in herds that may be of considerable size. This difference in gregariousness between sexes is characteristic of wapiti in general, and as such can be analyzed for its possible adaptive significance for the whole species. I have suggested that, for both sexes, herd size reflects throughout the year the patterns of behaviour established during the rutting seasons. For successful reproduction, females need to "want" to aggregate, while males do not mingle with other males. It is to the reproductive advantage of each individual to maintain, during non-reproductive times, the sex-specific patterns of behaviour so essential for successful reproduction.

With regard to sex segregation, the theory proposed by Morgantini and Hudson (1981) for bighorn sheep has been applied to wapiti. The theory maintains that the mixing of males and females outside the rutting season could result in sexual harassment of females and in male fights, at times when reproduction is impossible. Therefore, the males actively avoid female herds, as demonstrated by historically reported instances of males initially colonizing an area, to be displaced by the arrival of colonizing female herds. In addition, the results of this study indicate that there is no actual habitat segregation, but mostly spatial separation between the sexes.

6.2. Concluding remarks

Wapiti apparently evolved in cold, northern environments, characterized by a high temporal hetereogeneity. These environments favored species with a broad ecological niche (Levins 1968). Until decimated in the last one hundred years, wapiti have proven to be a very successful species, as demonstrated by their wide distribution, large population numbers, and widespread use of different environments. Thus, they have adjusted very succesfully to the northern environment.

Geist (1982) states that wapiti, because of their recent evolutionary history, have not had time "to evolve a close fit between adaptive strategies and the environment". In effect, the results of this study demonstrate that wapiti as a species do not show fixed behavioural adaptations to any given environment, but a flexibility that allows individuals to use different adaptive strategies under the same environmental conditions. However, I maintain that this flexibility, instead of representing a poor fit to the environment, represents the major behavioural adaptation of wapiti. That is, through the ability to respond with flexibility to the challenges of reproduction and survival, it allowed their successful colonization of North America.

"The capacity to react differently to the environment is often so complex .... that gene patterns ... (must be) the product of long periods of selective sorting." (Allee et al. 1949). The behaviour of higher animals cannot be reduced to direct responses to simple stimuli. Strongly instinctive and genetically predetermined specialized behaviour would be a liability under conditions that may quickly vary in time and space. Instead, wapiti have followed the path of generalization and flexibility.

The study of the adaptive significance of behavioural patterns in wapiti carries the risk of confusing causes with effects and with mere coincidences. Wide-sweeping, stereotypic generalizations about how a wapiti is expected to behave, or what it is expected to do, may limit instead of enhance the ability of wildlife biologists to understand and manage this species. The individual variations and different adaptive strategies of wapiti present a challenge to wildlife students and managers, to carefully observe and analyze local populations, and use the same flexibility in taking management decisions, as this species will in its reactions to the environment.

6.3. Literature cited.

ALLEE, W. C., A. E. EMERSON, O. PARK, T. PARK, and K. P. SCHMIDT. 1949. Principles of animal ecology. W.B. Saunders, Philadelphia and London. 837pp.

BELOVSKI, G. E. 1981. Optimal activity times and habitat choice of moose. Oecologia 48: 22-30

CODY, M. L. 1974. Optimization in ecology. Science 183: 1156-1164.

DAVIES, N. B., and A. I. HOUSTON. 1984. Territory economics. in J. R. Krebs and N. B. Davies (Eds.), Behavioural ecology. 2nd ed. Blackwell, Oxford.

FESTA-BIANCHET, M. 1987. Individual reproductive success of bighorn sheep ewes. Ph.D. Thesis, Univ. Calgary, Calgary, Alberta. 229pp.

GEIST, V. 1982. Adaptive behavioral strategies. Pages 219-278 in J. W. Thomas and D. E. Toweill (Eds.), Elk of North America. Ecology and management. Stackpole Books, Harrisburg, Pa.

LEVINS, R. 1968. Evolution in changing environments. Princeton Univ. Press, Princeton. 120 pp.

McCLEERY, R. H. 1978. Optimal behaviour sequences and decision making. Pages 377-410 in J. R. Krebs and N. B. Davies (Eds.), Behavioural ecology. An evolutionary approach. Blackwell Scientific Publications, Oxford.

McFARLAND, D. J. 1977. Decision making in animals. Nature 269: 15-21.

MORGANTINI, L. E., and R. J. HUDSON. 1981. Sex differential in use of the physical environment by bighorn sheep (Ovis canadensis). Can. Field Nat. 95:60-74.

OWEN-SMITH, N., and P. NOVELLIE. 1982. What should a clever ungulate eat. Am. Nat. 110: 151-178.

PYKE, J. H. 1984. Optimal foraging theory: a critical review. Ann. Rev. Ecol. Syst. 15: 523-575.

SIBLY, R., and P. CALOW. 1986. Why breeding earlier is always worthwhile. J. Theor. Biol. 123: 311-319.

APPENDIX A.

ANIMAL NUMBERS AND TRENDS

1. POPULATION LEVELS

1.1. Historical perspective

Documented evidence on historical wapiti population levels within the Panther-Red Deer and Clearwater region is limited.

In the early 1800s, in the area that is now within the boundary of Banff National Park, records of the presence of wapiti are limited to the observations by Alexander Henry near the confluence of the Howse and North Saskatchewan Rivers (Coues 1897). In 1842, wapiti were reported along the Bow River (Simpson 1847). However, in 1858, the Palliser expedition (Spry 1963) did not find wapiti along the Bow and the North Saskatchewan River valleys. According to Indians encountered on the trail, wapiti along the North Saskatchewan River valley had been decimated in 1847 by a "disease" that followed an extensive wild fire (Spry 1963). In 1859, the Palliser expedition, while not recording any wapiti sign along the Pipestone River, killed one animal in the upper Siffleur River valley, and observed several tracks along the North Saskatchewan River, west of the Kootenay Plains. In 1906, the Superintendent of Banff National Park (then Rocky Mountains Park) reported "...a good number of big game in the Park consisting of moose, elk..." (Green 1946).

Outside the eastern boundary of Banff National Park, in

1800, David Thompson observed that wapiti were "plentiful" along the Red Deer River, probably outside the Eastern Front Range of the Rocky Mountains, 20 miles east of the Ya Ha Tinda Ranch. In 1810, Alexander Henry hunted them on the Kootenay Plains (Hopwood 1971, Coues 1897). In 1904, George Harrison reported a large number of old wapiti antlers on the Ya Ha Tinda Ranch (McGillis 1976). However, twelve years earlier, in 1892, Coleman (1911), following old Stony Indian trails from Morley, north-west of Calgary, up the Red Deer River valley, through the Ya Ha Tinda Ranch area and across the Clearwater River, to the North Saskatchewan and the Kootenay Plains, did not find any sign indicating the presence of wapiti.

Apparently, by the late 1800' and early 1900s, due to a combination of severe winters and indiscriminate hunting by white men and indians (Stutfield and Collie 1903, Millar 1915, Soper 1970), wapiti had almost disappeared from the Canadian Rocky Mountains. In central western Alberta, the only remnant population, reduced to a few individuals, was found in the Brazeau drainage (Millar 1915, Stelfox 1964).

The present wapiti population in the region is believed to have originated from the release of about 245-251 animals in Banff National Park, mostly along the Bow River valley, between 1917 and 1920 (Lloyd 1927, Green 1946). This introduced stock interbred with native wapiti, and, possibly, with wapiti moving into Banff National Park from British Columbia (Holroyd and Van Tighem 1983). The herd rapidly increased and colonized adjacent valleys (Chapter 3). By the late 1930s, wapiti were common throughout the National Park. Banff National Park Warden's reports (BNP files) indicate that wapiti were present along the Panther, Red Deer and Clearwater Rivers in the 1940s and early 1950s. However, there is no record of their numbers.

In 1941, in response to perceived overpopulation, range deterioration and competition for forage with bighorn sheep (Cowan 1943, 1944, Green 1946, Tanner 1950), an extensive slaughter program was initiated. National Park documents (Holroyd and Van Tighem 1983) indicate that, during several years, the removal program was questionable since Park Wardens were reporting less animals than they were ordered to kill. Nonetheless, by 1969, when wapiti slaughters were terminated, a total of at least 3,923 animals had been removed (Holroyd and Van Tighem 1983).

Outside Banff National Park, the first recorded observation of wapiti in the Panther-Red Deer-Clearwater region was in 1933 on the Ya Ha Tinda Ranch (Cowan 1944). Ten years later, during the winter of 1942-43, a herd of 50-60 bulls were reported wintering on the Ranch and surrounding areas, while cows wintered further east, along the James River (McGillis 1976).

1.2. From the 1950s to the present time

During the last 35 years, the Panther, Red Deer and Clearwater River drainages have supported a large wapiti population. Unfortunately, records of its size and distribution are either lacking or inconsistent. Nonetheless, based on various reports, and on the present study, the following can be ascertained.

1.2.1. Banff National Park

Until 1975, estimates of the wapiti population inhabiting the Red Deer-Panther-Clearwater region in Banff National Park were based on occasional ground observations by Park Wardens during their backcountry patrols. Systematic ungulate winter aerial surveys of the National Park were carried out from 1975 to 1977. In the Panther and Red Deer River drainages, five wapiti were counted in 1975, 33 in 1976 and 189 in 1977. The apparent increase is difficult to explain. Jacobson (1977) noted that, during the first two winters, surveys were conducted "under optimum conditions" and not "very many tracks" were observed. However, at the time, the surveys did not consider that almost the entire wapiti population in the region winters outside Banff National Park, and that winter movements across the Park boundary can occur. Hence, surveys limited to the National Park could not provide a reliable estimate of the wapiti population in the region.

Between 1983 and 1987, attempts were made to survey both inside and outside Banff National Park. The results will be discussed in Appendix A, Chapter 1.2.3.

1.2.2. Clearwater River (outside BNP).

No record on the number of wapiti is available prior to 1955. On December 7, 1955, the Alberta Forest Officer's Annual Game Report for the year reported 370 wapiti east of Elk Creek (approximately 40 km from the eastern boundary of Banff National Park), but only "three small herds" between Elk Creek and the National Park boundary (Edgecombe 1955). In January 1957, 439 wapiti were counted in the same area, but no reference was made to the region west (Lyle 1957). The abundance of wapiti along the eastern portion of the Clearwater River valley is further indicated by the large number of animals taken legally by hunters and checked by the Clearwater Forest Ranger Station. Between 1957 and 1960, the total reported harvest amounted to 672 animals, 245 males and 357 females. The highest harvest was recorded during the 1959 season, 146 males and 154 females (Loblaw 1960). In 1961 and 1962, the legal harvest, based on animals checked at the Ranger Station, averaged 100 animals per year. However, Forest Rangers noted that, in addition, "...indian hunters took quite a number...between January 1st and August 31st" (Loblaw 1962). In 1962, that number was estimated at about 56 animals (Kay 1963). At this time the wapiti population in the area was believed to be decreasing (Longworth 1963).

With regard to Harrison Flats, 10 km from the eastern boundary of Banff National Park, a Forest Officer for the Clearwater District during the early 1960s reports that, at that time, the area was used mostly by bulls, while females wintered further east (Loblaw per. com.). This observation is consistent with aerial surveys conducted by R. Webb of the Alberta Fish and Wildlife Division. On January 1962 and 1963, Webb reported 50 and 75 adult bulls, respectively, wintering on Harrison Flats (_in_ Flook 1970).

At the present time large herds of cows are known to winter on Harrison Flats and in the Lost Guide Creek area (2-5 km east of Harrison Flats), while only a few animals are reported wintering east, on historical winter ranges.

From 1977 to 1987 the wapiti population in the Harrison Flats area ranged between 150 to 250 animals (Bruns 1979, LeBlanc 1983, Morgantini and Russell 1983, Olsen and Bruns 1987).

1.2.3. Red Deer and Panther Rivers (outside BNP).

In 1942-43 only bulls wintered along the Red Deer River on the Ya Ha Tinda Ranch (Cowan 1944). Cows were found further east (McGillis 1976). However, in 1950, the Ya Ha Tinda Ranch was reported to winter approximately 100 cows, but no adult bull (Flook 1970). Since then, the wapiti population wintering on the Ranch has consisted mostly of cows, calves and yearling bulls.

Prior to the 1960s, there is no official record of the numbers of wapiti along the Panther River, between the Eastern Front Ranges and the boundary of Banff National Park. In 1956, Jacobson (pers.comm.) counted more than 400 animals in the Corners area and along DogRib Creek.

The presence of adult bulls on the Ya Ha Tinda Ranch and on Harrison Flats in the early 1940s and 1950s has been interpreted by Flook (1970) as reflecting the colonization of new ranges by the wapiti population of Banff National Park. In this regard, it has been observed that wapiti and red deer males are the first to colonize new areas (Cowan 1944, Darling 1955). However, the concomitant presence of cow herds further east of both Harrison Flats and the Ya Ha Tinda Ranch area does not support Flook's (1970) interpretation. The absence of wapiti in the region in the early 1900s suggests that these herds originated from the animals reintroduced along the Bow River valley in Banff National Park. This is further indicated by historical records (Chapter 3) and by the long seasonal migrations that most of the wapiti population undertakes every year (Chapter 3). The presence of bulls in the 1940s and 1950s on ranges where at the present time mostly cows are found simply reflected spatial separation between the two sexes (Chapter 5). The different distribution of wapiti in the 1960s and 1970s indicate that an effective reduction of historical wapiti ranges occurred along the Clearwater and the Red Deer Rivers, possibly related to increased human activities along the Forestry Trunk road. Large herds of females now winter on ranges previously occupied by males, while the latter have moved further west and winter on more rugged terrain. A similar range reduction may also have occurred along the Panther River. However, no historical record on wapiti numbers in this river valley is available.

During the 1950s the number of wapiti observed in winter on the Ya Ha Tinda Ranch apparently increased to reach a total of 1,400-1,800 individuals in April 1961 (Webb 1961). However, several counts were estimates from ground surveys and, according to Webb (1961), some of them were "highly colored". Further, Webb (1961) stated that

> "...at no time were there more than 1,200 elk on the Ranch area...This peak was reached in April and sustained for a relatively short period....I am still at loss to completely explain the 1,200 count in April. It is 400 higher than the previous high of 800 obtained in February 1959. According to harvest and increment figures the total should still be near 800. It is possible that a portion of the "Corners" (Panther-Dormer Rivers junction) herd crossed over the Ranch to supplement the herds already there. At any rate elk arrived on the Ranch this year that normally winter elsewhere." (Webb 1961).

From 1961 to the present, the number of wapiti observed on the Ya Ha Tinda Ranch region and in the "Corners" in winter have ranged from 1,400-1,800 (April 1961) to 399 (January 1975), to 1137 in 1983 (Table A.1). No comparison from year

A.1. Wapiti observed during aerial surveys of the Ya Ha Tinda-Panther River region outside Banff National Park. 1973-1988

1973	January*	422
	March**	1,023
1974	January*	467
	February*	418
1975	January*	399
	February*	586
1976	January*	449
	March*	600
1977	March*	381
1978	February*	619
1979	February*	636
1980	February*	506
1982	March*	521
1983	February*	422
	March**	1,023
1984	March*	1,058
1985	March*	832
1987	January*	1,187
	February**	1,372
1988	March*	1,297

* Alberta Fish and Wildlife survey
** Banff National Park survey

Sources: Alberta Fish and Wildlife files
Banff National Park Files

to year can be made since surveys were conducted in different months with different weather conditions. In February 1975, for instance, after a harvest of 108 animals during a special winter hunting season, 586 wapiti were counted, versus 399 counted only one month earlier. In 1983, an aerial survey carried out in January by the Alberta Fish and Wildlife Division counted only 200 animals on the Ya Ha Tinda area and 222 in the "Corners". However, two months later, in March, an aerial survey carried out by the Banff National Park Wardens Service in cooperation with the Alberta Fish and Wildlife Division counted 675 wapiti in the Ya Ha Tinda Ranch area and 348 in the Corners. These figures underline the unreliability of any one single survey taken in isolation. The movements of wapiti across the National Park boundary further undermine the reliability of surveys conducted only over the Province or the National Park. It should be also emphasized that when aerial surveys refer to the Ya Ha Tinda or to the Corners they do not refer specifically to the Ya Ha Tinda Ranch or to the Corners meadows, but include wapiti found over a large territory within the Red Deer and Panther River drainages, respectively.

An attempt to integrate wapiti surveys along the Red Deer and the Panther Rivers with surveys carried out in Banff National Park along the same river valleys was initially carried out by Jacobson (1977) and is shown in Table A.2. This summary shows a major drop in the wapiti population in

Table A.2. Wapiti surveys along the Red Deer and Panther River drainages, outside and inside Banff National Park. 1973-1977. Aerial surveys data.

Area	1973	1974	1975	1976	1977
WMU 416* (Panther Riv.)	119	199	130	132	2
WMU 418* (Red Deer Riv.)	807	268	264	284	308
Banff N.P.*	-	-	5	33	189
Totals*	926	467	399	449	499
Fish & Wildl. Surveys**	727(May)	418(Feb)	586(Feb)	416(Mar)	535(Feb)

* January data. Source: Jacobson 1977.
** Excluding Banff National Park.
Sources: Hall et al. 1973, 1974, 1975; Bruns 1979; Nette 1983.
WMU: Wildlife Management Units.

the region between 1973 and 1974. The decrease is also shown by surveys carried out by the Alberta Fish and Wildlife Division (Hall *et al*. 1975). It coincides with a winter (1973-74) characterized by heavy snowfall in November and January. However, there is no record showing extensive winter kill. It is possible that the difference in numbers between 1973 and 1974 is partially due to aerial survey bias and animal dispersal over the region. Nonetheless, the relatively consistent number of wapiti observed from 1974 to 1977 indicate that indeed the population in the area was lower than it was in the 1960s. This may have been caused by a combination of severe winters (1969-70; 1971-72; 1973-74) and special winter hunting seasons (1969-1975), during which 674 animals were harvested.

During this study, 1976-1980, the number of wapiti wintering on the Ya Ha Tinda Ranch ranged from 350 to 450 animals. On the "Corners", the population was estimated at about 100-150.

Between 1980 and 1983, the number of wapiti in the region varied from 521 to 422. Between 1984 and 1988, ground and aerial counts (Table A.1) indicated the presence of a significantly higher number of animals. However, these data are difficult to interpret, since wide variations are present, even between one month and the next (e.g. February-March 1983). Nonetheless, by using only the highest number of wapiti counted per year the following can be determined. The difference between the highest numbers of wapiti counted in 1983 (1,023 animals) and in 1987 (1,372 animals), shows a 8.5% yearly population increase over a 4 year-period (Table A.3). The yearly increment over a 3-year period (1984-1987) amounted to 6.9 %. Inclusion of wapiti counted in the Clearwater region in the analysis shows a 8.3 % yearly increment over the same 4 year period, and 5.1 % yearly increment over the 3 year-period (Table A.3). These yearly increment values cannot be considered representative of the yearly increase of wapiti in the region. For instance, in February 1985, 96 animals were trapped and removed from the area. Further, unregulated hunting (native hunting and poaching) and wolf predation remove an unknown number of animals that can vary from year to year.

The lower number of animals counted in 1988, compared to the 1987, is difficult to explain. The 1988 survey of the Red Deer-Panther region observed 1,297 wapiti. This number is 75 animals less than the number of animals counted in 1987 (1,372), and 170 animals less than it should have been expected assuming a conservative yearly increase of 6.9% (1,467). The difference between the two years may reflect a higher mortality as well as aerial visibility bias.

Table A.3. Highest numbers of wapiti counted in the Red Deer-Panther-Clearwater region between 1983 and 1987, and estimated increment rates.

	March 1983	March 1984	February 1987
Red Deer River*	675	1,058	939
Panther River**	348	79	433
TOTALS	1,023	1,137	1,372

Average yearly increment rates.

1983-1987: 8.5%
1984-1987: 6.9%

Clearwater River***	159	228	204

Average yearly increment rates for the entire region.

1983-1987: 8.3%
1984-1987: 5.1%

Source: Olsen and Bruns 1987.
Skjonsberg 1988

1.2.4. Conclusions

Overall, analysis of aerial and ground surveys during the last 20 years underlines the problems that wildlife biologists face in assessing wapiti population in the region, and particularly on the Ya Ha Tinda Ranch. Unusual snowfall, as it may have been the case in 1961 (Webb 1961), human activities and range depletion on other ranges, both inside and outside Banff National Park, may force wapiti onto the Ya Ha Tinda Ranch. As it is indicated by the present study, wapiti may move in winter to the Ya Ha Tinda Ranch from ranges 30 km east, and from the Clearwater and the Panther Rivers. Further, the wapiti herds along the Clearwater, Red Deer and Panther Rivers may intermingle on summer ranges with wapiti inhabiting the Ram River region, British Columbia and the Cascade River valley, respectively. It is reasonable to assume that range loss in those areas, or an increase in population size, could result in an increase in the number of animals in the Clearwater-Red Deer-Panther region. Estimates of population size in the region are also confounded by visibility biases associated with aerial surveys. Therefore, while population trends over numerous years can be detected, yearly population levels cannot be determined accurately enough to assist yearly management decisions.

2. PREDATION AND HUNTING LOSSES

2.1. Predation

There is little knowledge about the presence of predators in the Red Deer-Panther-Clearwater region before the 1970s. In the early 1970s, 2 wolves were reported ranging over the Ya Ha Tinda Ranch. However, there is no information about predation pressure on the wapiti herd that wintered in the area. It is likely that, at the time, the wolves were living off the large number of wapiti wounded during special winter hunting seasons (Appendix A, Chapter 2.2).

Between 1976 and 1980, predation on the wapiti population in the region was minimal (this study). Signs and activities by wolves were seldom recorded. Similarly, in spite of continuous intensive field efforts to locate newborn calves on winter and intermediate ranges, black and grizzly bears, or signs of their activity, were never encountered. Although bears were active in the summer, their low density, and the use by wapiti of wide open habitats, limited the impact of predation. One instance of a bear approaching a nursery herd was indeed recorded. However, cows and calves were 500 m away by the time the bear reached their bedding site.

Since the early 1980s, a pack of wolves numbered from 5 to 9 animals has been reported in the Ya Ha Tinda Ranch region (Banff National Park Files, Alberta Fish and Wildlife Files).

The pack ranges from the National Park boundary to Eagle Lake, and from Ribbon Flats, south of the Ranch, to the headwaters of Scalp Creek. There are no data on the number of wapiti killed by wolves. However, Ya Ha Tinda Ranch personnel estimate that, in the area, wolves kill an average of some 10-20 animals every winter. It is also possible that wolves feed on animals wounded or killed by native hunters.

2.2. Hunting and poaching

2.2.1. Regulated hunting

The wapiti population along the eastern boundary of Banff National Park has been subjected to various degrees of hunting pressure. Consistent records of harvest are not available.

Prior to 1975, there is little available information on the total number of animals hunted during regular fall seasons. At the time, compulsory registration of kill was not required. Records of wildlife harvest in the region were maintained by the Alberta Forest Service during the 1950s and 1960s. However, the only records which are still available refer to the Clearwater River between 1957 and 1962 (Appendix A, Chapter 1.2.2.).

At the present time, wapiti hunting in the fall is restricted to trophy males (Table A.4.).

Information on winter hunting seasons is also limited. The only record I was able to find on the number of wapiti

Table A.4. Trophy wapiti harvest during the fall in Wildlife Management Units 416, 418 and 420. (1975-1987).

WMU	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987
416	6	0	12	34	6	25	3	28	17	45	69	36	4
418	3	3	10	7	11	27	4	32	26	35	32	33	22
420	7	4	7	11	16	25	17	37	32	27	23	22	26
Total	16	7	29	52	33	77	24	97	75	107	124	91	52

Sources: Alberta Fish and Wildlife Files.
Note, these records are based on hunter registrations. The WMU location of several kills may be inaccurate.

WMU 416: Panther River watershed, from BNP boundary to approximately the confluence of the Panther and Red Deer Rivers and the Forestry Trunk Road.
WMU 418: Red Deer River watershed, from BNP boundary to the skyline of the Eastern Front of the Rocky Mountains.
WMU 420: Clearwater River watershed, from BNP boundary to the Forestry Trunk Road.

hunted in winter before 1969 refers to 1962, when, on the Ya Ha Tinda Ranch, an open season was declared. Nine hundred hunters registered in the first day, 43 wapiti were taken (Sundre Round-Up, Vol 2, No 52, January 1962).

Between 1969 and 1977, in response to presumed overgrazing conditions on the Ya Ha Tinda Ranch, special winter hunting seasons were held along the Red Deer and the Panther Rivers. The total legal harvest is summarized in Table A.5. These figures are largely conservative. Because of the facility with which hunters contacted herds of cows and calves in the area, "flock shooting" was common (Alberta Fish and Wildlife Files). A substantial, unreported number of animals were wounded and presumably died later (see Marty 1978: 238-249). In 1978 the special winter season was discontinued.

2.2.2. Unregulated hunting

Unregulated hunting includes hunting by natives and poaching, and it can occur at any time of the year.

Native hunting is concentrated toward areas that offer easy motorized access. In the Red Deer-Panther-Clearwater region, the Ya Ha Tinda Ranch offers easy access and, in winter, supports a high density of wild ungulates.

There are no data on the level of native hunting pressure on wapiti prior to the winter of 1975. Between 1975 and 1978, natives did not hunt in the area. However, during the winter

Table A.5. Wapiti harvest during special winter hunting seasons on the Ya Ha Tinda Ranch (WMU 418) and the Corners (WMU 416) areas.

	1969	1970	1971	1973	1974	1975	1976	1977
Bulls	15	32	25	25	23	16	16	17
Cows	59	62	75	104	98	86	-	-
Calves	4	14	12	6	12	6	-	-
Total	78	108	112	135	133	108	16	17

Sources: Alberta Fish and Wildlife Files

Notes:
1 week = 3 day hunt.

1969, 1970: 6 wk season (50 licences/wk)
1971, 1974: 4 wk season (290 licences)
1973: 4 wk season (280 licences)
1975: 4 wk season (1st wk bull only; 282 licences)
1972: no special season held
1976, 1977: bulls only. 286 licences per year.

of 1978-79, a minimum of 50 wapiti were taken. Since then, every winter natives have hunted on the Ya Ha Tinda Ranch. There is no accurate count of the number of animal taken. Based on personal counts and on occasional observations by Ranch personnel, the minimum number is believed to range between 50 and 100 animals. This number does not include the animals that may be wounded and later die.

Poaching on the Ya Ha Tinda Ranch is very rare due to the presence of Ranch personnel who consistently patrol the area while monitoring the movement of horses. However, in view of the remoteness of most of the Red Deer-Panther-Clearwater region, during the regular trophy hunting season, some illegal hunting may occur.

3. POPULATION PRODUCTIVITY

3.1. Cow-calf ratios

During this study, an attempt was made to determine calf production through extensive summer classification counts. Every month the number of new-born calves present in different herds inhabiting separate valleys was assessed. A total of 138 female herds (2,043 animals) were classified (Table A.6).

Between 1977 and 1979, the number of calves in the summer ranged between 26 and 31 per 100 cows (including female yearlings). No statistical difference is found between months

Table A.6. Calf/cow ratios of the wapiti population in the Panther-Red Deer-Clearwater region. 1977-1979.

		July			Aug.			Sept.			Winter	
		1977	1978	1979	1977	1978	1979	1977	1978	1979	1978	1979
Calf/cow herds	N	247	191	321	177	267	223	197	136	161	368	510
	n	16	6	11	9	15	12	19	10	12	4	5
	$\bar{x}$	15	32	29	20	18	19	10	14	13	92	102
	cow/calf ratio	.34	.32	.27	.32	.32	.29	.33	.32	.29	.29	.28
Barren cow herds	N	12	14	10	16	8	11	21	17	14	–	–
	n	10	4	4	3	4	3	7	3	3	–	–
	$\bar{x}$	1	3	2	5	2	4	3	6	5	–	–
Calf/cow ratio over total female population		.31	.29	.26	.29	.30	.28	.30	.28	.27	.29	.28

N = Total number of animals classified
n = number of herds
x = average herd size

and years. The apparently lower calf production in the summer of 1979 is probably due to the inherent sampling error associated to classification counts (Kimball and Wolf 1974).

In spite of continuous attempts, large herd sizes (100-500 animals) on winter ranges precluded accurate winter classification counts. The only reliable calf/cow ratios were obtained on March 6, 1978 (4 herds, 368 animals) and February 17, 1979 (5 herds, 510 animals), when calf production averaged, respectively, 29 and 28 calves per 100 cows (Table A.6).

These results are consistent with recent summer aerial surveys carried out by the Alberta Fish and Wildlife Division along the eastern slopes of the Rocky Mountains between the Panther and the Brazeau Rivers (Nette, 1983: calf/cow ratio of 29 calves per 100 cows, N=527) and with late winter counts conducted on the Ya Ha Tinda Ranch in 1982 and 1983 (LeBlanc 1983: calf/cow ratio of 16 and 31 calves per 100 cows). Similar calf/cow ratios were also reported in late fall 1977 along the Bow River valley (Jacobson 1977: 31/100) and in the fall of 1960 in Banff National Park by the Wardens Service (Flook 1970: 28/100).

Calf production by the wapiti population inhabiting the Panther-Red Deer-Clearwater region is markedly lower than observed in other areas. Summer calf/cow ratios of 40/100, 54/100 and 51/100 have been reported in soutwestern Alberta

(Kansas and Pall 1983), western Montana (Marcum 1980) and Utah (Kimball and Wolf 1974). However, summer calf/cow ratios comparable to those observed in the study area have been reported by Knight (1970: 29-32/100) in the Sun River herd in Montana.

Low calf production has been related to several factors, such as intrauterine mortality and low survival of newborn calves due to inadequate winter nutrition of cows (McNeil 1972, Thorne _et al_. 1976), predation (Schlegel 1976) and winter calf losses (Cowan 1950).

As previously mentioned (Appendix A, section 2.2), predation on the wapiti population in the Panther-Red Deer-Clearwater region between 1976 and 1979 was practically non-existent.

Wapiti along the Panther, Red Deer and Clearwater Rivers winter on ranges characterized by relatively mild weather conditions (Chapter 2). During this study, snow depth on the open grasslands never exceeded 15 cm and, due to the ameliorating influence of warm westerly winds, it persisted for only a few days following snow storms. The ranges are considered in good conditions and able to support higher population density (McGillis 1976). Overwinter losses were not recorded.

Minimal calf losses due to predation or winter weather conditions are further indicated by the little significant change in calf/cow ratios over the summer and through the winter (Table A.6).

3.2. Pregnancy rates

During this study, pregnancy rates were not assessed. However, from 1969 to 1975, late winter hunting seasons were conducted along the Panther and the Red Deer Rivers, outside the National Park. Based on data collected by the Alberta Fish and Wildlife Division through a hunter check station (Paulsen 1975), the average pregnancy rate for all years and age classes combined was 66% (Table A.7). The pregnancy rate for 306 animals older than yearlings was 76%.

Yearly comparisons cannot be carried out due to small sample sizes.

Pregnancy rates should be considered minimal since some hunters may have been unwilling to collect fetuses (Nette 1983). Nonetheless, pregnancy rates of yearlings (16%) and two year olds (74%) compare favorably with values reported for other populations (Buechner and Swanson 1955, Kimbal and Wolf 1974, Taber et al. 1982). Pregnancy rates in mature cows (3 3/4 - 10 3/4 year old: 76%) appear lower than those of most other herds (Taber et al. 1982: 84-100%). Similar low average pregnancy rate has been reported in Elk Island National Park (Carbyn 1975: 66%).

Low pregnancy rates have been associated with

Table A.7. Pregnancy rates of female wapiti in late winter along the Panther and the Red Deer Rivers. 1969-71 and 1973-1975. (modified from Paulsen 1975).

Age	Animals harvested	Number pregnant	Percentage pregnant
1 3/4	25	4	16
2 3/4	42	31	74
3 3/4 - 5 3/4	141	106	75
6 3/4 - 10 3/4	88	69	78
over 10 3/4	35	28	80
unknown	86	38	44
Total	417	276	66

overpopulation and poor food supply (Cowan 1950, Buechner and Swanson 1955, Greer 1966, Gross 1969). Severe winter weather in the early seventies and perceived overgrazing conditions on winter ranges (Neave 1969) cannot explain the low pregnancy rates of mature cows in the Panther-Red Deer-Clearwater region. Average midwinter bone marrow fat of wapiti during the same period was fairly high, ranging between 85 and 94% (Paulsen 1975). Knight (1970) suggested that low calf production could also reflect an older age structure and, hence, lower fertility rates of lightly hunted populations. The author did not have fertility rates and age structure data to support his hypothesis. Nonetheless, winter harvest data for the Panther-Red Deer herd between 1969 and 1975 indicate a young age structure with older cows (over 10 3/4 year old) averaging 10% of the total harvest (Table A.7). Their pregnancy rate was the highest of all age groups.

During this study, the average pregnancy rate may have been conceivably higher due to lower population levels, mild winter weather and good range conditions. However, even considering the low average pregnancy rate of the early seventies (66%) as representative for the wapiti herd in the region, comparison with calf/cow rates of early summer (29-32/100) indicates a high calf mortality. Apparently, sometime between late pregnancy (February) and one month after birth (July), about 45% of the potential calf production is lost.

For the cow-yearling herd wintering on the Ya Ha Tinda Ranch (app. 450 animals between 1976 and 1980), the loss amounts to some 134 calves. As previously mentioned (Appendix A, Chapter 2.1.), during the study predation was minimal. Wolves and bears were not present on the Ya Ha Tinda Ranch, while coyotes were not a significant mortality factor for newborn calves due to their low number (5-10 animals) and to the observed highly protective behaviour of cows. Even though instances of predation may have been missed, the evidence suggests that most of the calf loss of the wapiti population of the Panther-Red Deer-Clearwater region may be occurring prior to birth (resorption or abortion) or at birth (still-death). The loss may be related to the severe mineral deficiency in the winter diet of the animals in the region, particularly phosphorus (Morgantini and Russell 1983).

3.3. Population productivity model

During this study, in order to better understand the performance of the cow-calf herd that winters on the Ya Ha Tinda, a computer simulation model was developed. The hypothetical female herd was structured in 14 age groups. No cow lived beyond 14 years of age. Fecundity rates were the pregnancy rates of the early 1970s, with 75% of all adult cows, 69% of all two-year old cows, and 16% of all yearling cows producing a calf. The initial population consisted of

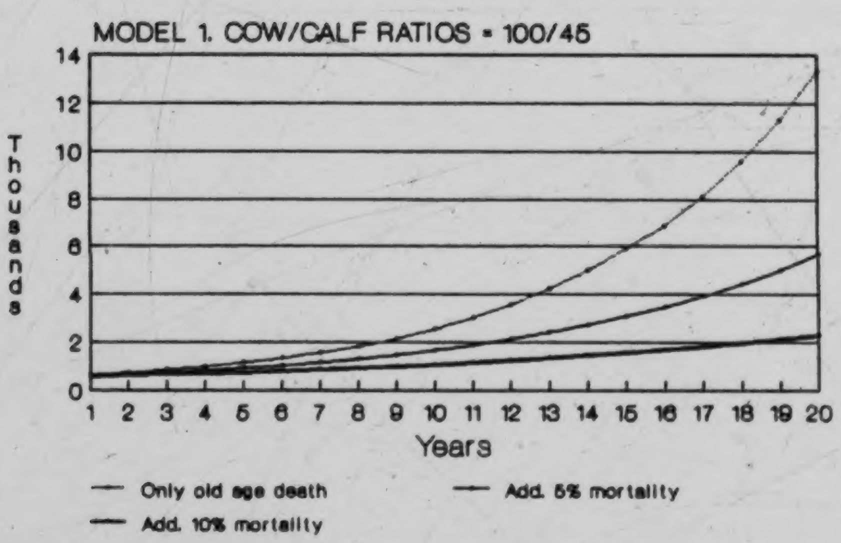
457 cow-calf-yearlings with a cow/calf rate of 100:33. However, after the first year, cow/calf rate reflected the high pregnancy rates and increased to above 45 calves per 100 cows.

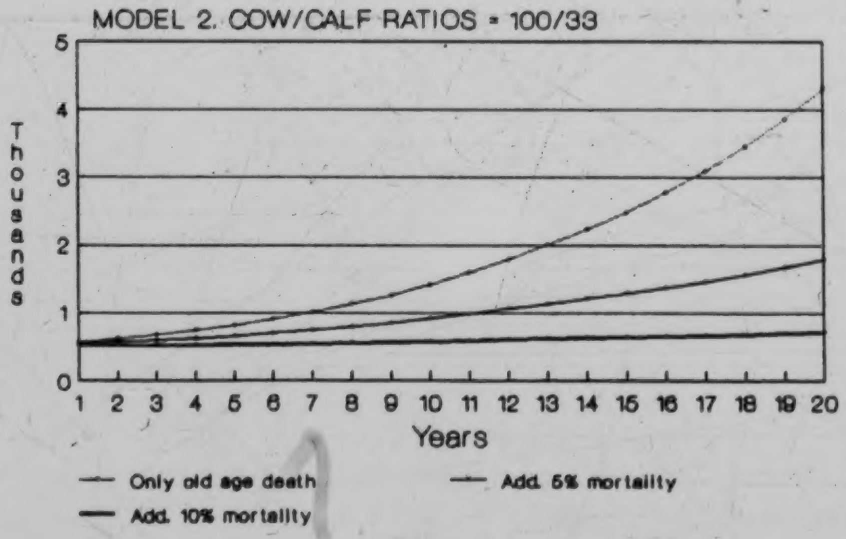
Two different population models were simulated. In the first one, calf mortality was set at 20% of the calf crop. In the second, in order to reach the low cow/calf rates observed in the study area, calf mortality was increased to reach 45%. The performance of the herd in each of the two models was tested for three different cow mortality rates: 1. Only old age death (approximately 5% of cows two-year old or older); 2. Old age death plus 5% mortality; 3. old age death plus 10% mortality. The results are presented in Figure A.1.

The first model is not really representative of the herd on the Ya ha Tinda Ranch, since cow/calf rates are significantly higher than those observed in the field. Nonetheless, it shows that such herd may stand a mortality of 10% additional to old age death, and still increase at a rate of 7.2% per year.

In the second model, maximum yearly increment rate (with no animal loss beside old age) averages 11.6%. Five and 10% additional mortality will lower the increase to 6.7% and 1.8% per year. A population simulation model is only intended to better understand the performance of populations in the field, and does not pretend to emulate the natural world. In this

FIGURE A.1. Population model of two wapiti female herds under three different levels of mortality.


MODEL 1. COW/CALF RATIOS = 100/45
Thousands
0
2
4
6
8
10
12
14
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
Years
Only old age death
Add. 5% mortality
Add. 10% mortality


MODEL 2. COW/CALF RATIOS = 100/33
Thousands
0
1
2
3
4
5
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
Years
Only old age death
Add. 5% mortality
Add. 10% mortality

context, it is interesting to note that the increment values of the population in the model compare reasonably well with the performance of the wapiti population in the Red Deer-Panther-Clearwater region (Table A.3). Five-ten percent mortality in a female herd of 1000 individuals represent 50 to 100 animals. On the Ya Ha Tinda Ranch, native hunting and, at the present time, wolf predation, most likely remove as many animals.

4. Literature cited

BRUNS, E. H. 1979. Region 3 Elk survey of known winter ranges. Alberta Fish and Wildlife Division Files. Edmonton. 7pp.

BUECHNER, H. K., and C. V. SWANSON. 1955. Increased natality resulting from lowered population density among elk in southeastern Washington. Trans. North Amer. Wildl. Conf. 20: 560-567.

CARBYN, L. N. 1975. Wolf predation and behavioral interactions with elk and other ungulates in an area of high prey diversity. Ph. D. Thesis. Univ. Alberta, Edmonton. 234pp.

COLEMAN, A. P. 1911. The canadian rockies. New and old trails. Henry Frowde, Toronto. 383pp.

COUES, E. E. 1897. New light on the early history of the greater northwest: the manuscript journals of Alexander Henry and David Thompson. New York, Francis P. Harper 2: 676-669

COWAN, I. MCT. 1943. Report on game conditions in Banff, Jasper and Kootenay Parks. Unpubl. rep. for National Parks Bureau. Univ. of British Columbia. Vancouver. 144pp.

COWAN, I. MCT. 1950. Some vital statistics of big game mammals of western Canada. Trans. N. Amer. Wildl. Conf. 15: 581-588.

DARLING, F. F. 1955. A herd of red deer. A study in animal behaviour. 2nd ed. Oxford Univ. Press, London. 215pp.

EDGECOMBE, A. H. 1955. Game report for the Clearwater District. Report to the Forest Superintendent, Rocky Mountain House, Alberta. Rocky Mountain House Forest Service Files. 1p.

FLOOK, D. R. 1970. Causes and implications of an observed sex differential in the study of wapiti. Canadian Wildlife Service. Rep. Ser. No 11. 71pp.

GREEN, H. V. 1946. The wapiti of Banff National Park - Unpubl. Rep. Can. Wildlife Serv. Edmonton. 32pp.

GREER, K. R. 1966. Fertility rates of the northern Yellowstone elk populations. Proc. West. Assoc. State Game and Fish Comm. 46: 123-128

GROSS, J. E. 1969. Optimum yield in deer and elk populations. Trans. N. Amer. Wildl. and Natur. Resour. Conf. 34: 372-387.

HALL, B., A. COOK, and G. GUNDERSON. 1973. Ya Ha Tinda elk survey. Unpubl. Rep. Alberta Fish and Wildl. Div. Edmonton. 6pp.

HALL, B., and A. COOK. 1974. Ya Ha Tinda Elk Survey. Unpubl. Rep. Alberta Fish and Wildlife Division Files. Edmonton. 7pp.

HALL, B., and A. BIBAUD. 1974. Ya Ha Tinda Elk Survey. Unpubl, Rep. Alberta Fish and Wildlife Division Files. Edmonton. 7pp.

HALL, B., A. BIBAUD, K. FROGGATT, and B. TREICHEL. 1975. Ya Ha Tinda elk survey. Unpubl. Rep. Alberta Fish and Wildlife Division Files. Edmonton. 7pp.

HALL, B., A. BIBAUD, A. COOK, and K. FROGGATT. 1975. Ya Ha Tinda elk survey. Unpubl. Rep. Alberta Fish and Wildlife Division Files. Edmonton. 7pp.

HOLROYD, G. L. and K. J. VAN TIGHEM. 1983. Ecological (biophysical) land classification of Banff and Jasper National Parks. Vol. III: The wildlife inventory. Canadian Wildlife Service. 444pp.

HOPWOOD, V. 1971. David Thompson: travels in North America 1784-1812. MacMillan Publ. 342pp.

JACOBSON, P. 1977. Aerial census of ungulates in Banff National Park. Unpubl. rep. Banff National Park Warden Service, Banff. 67pp.

KANSAS, J. L., and O. PALL. 1983. The 1981 summer elk survey of the East Slopes of Alberta - Bow River to Waterton Park (1-8 August, 1981). Alberta Energy and Natural Resources, Fish and Wildlife Division Files, Edmonton.

KAY, W. 1963. Annual big game report 1962. Report to the Forest Superintendent in Rocky Mountain House, Alberta. Rocky Mountain House Forest Service Files. 2pp.

KIMBALL, J. F., and M. L. WOLFE. 1974. Population analysis of a northern Utah elk herd. J. Wildl. Manage. 38: 161-174.

KNIGHT, R. R. 1970. The Sun River elk herd. Wildl. Monogr. No. 23. Washington, D.C.: The Wildlife Society. 66 pp.

LOBLAW, T. C. 1960. Annual big game report. 1959. Rep. to the Forest Superintendent in Rocky Mountain House. Alberta. Rocky Mountain House Forest Service Files. 1p.

LOBLAW, T. C. 1962. Annual big game report 1961. Report to the Forest Superintendent in Rocky Mountain House. Alberta. Rocky Mountain House Forest Service Files. 2pp.

LEBLANC, R. 1983. Elk winter ranges surveys for the Rocky Mountain House Region. Alberta Fish and Wildlife Division, Rocky Mountain House, Files. 4pp.

LLOYD, H. 1927. Tranfers of elk for restocking. Can. Field Nat. 41:126-127.

LONGWORTH, G. A. 1963. Annual big game report 1962. Report to the Forest Superintendent in Rocky Mountain House, Alberta. Rocky Mountain House Forest Service Files. 5pp.

LYLE, R. J. 1957. Big game winter grazing report. *In* Annual big game report to the forest superintendent in Rocky Mountain House. Rocky Mountain House Forest Service

Files. 12pp.

McNEIL, G. R. 1972. Elk management in the Clearwater region. Idaho Wildl. Rev. 24: 3-6

MARCUM, C. L. 1979. Summer-fall food habits and forage preferences of a western Montana elk herd. Pages 54-62 in M. S. Boyce and L. D. Hayden-Wing (Eds.), North American elk: ecology, behavior and management. Univ. Wyoming, Laramie.

MARTY, S. 1978. Men for the mountains. McClelland and Stewart. Toronto. 270pp.

McGILLIS, J. R. W. 1976. Range management of the Ya Ha Tinda Ranch. Canadian Wildlife Serice, Edmonton. Unpubl. rep. CWS-13-77, 75pp.

MILLAR, W. N. 1915. Game preservation in the Rocky Mountains Forest Reserve. Department of the Interior. Forestry Branch Bulletin No. 51. Government Printing Bureau. Ottawa. 69pp.

MORGANTINI, L. E. and W. B. RUSSELL. 1983. An assessment of three selected elk winter ranges in the Rocky Mountains region. Wildlife Resources Consulting Ltd. Prepared for Alberta Fish and Wildlife Division. Edmonton. 265pp.

NEAVE, D. J. 1969. The results of a late elk season on the corners (S416) and Ya Ha Tinda (S418) areas. Alberta Fish and Wildlife Files, Edmonton. 20pp.

NETTE, T. 1983. Elk Surveys (Summer 1983) of the Rocky Mountain House Area. Alberta Fish and Wildlife Files, Rocky Mountain House. 36pp.

OLSEN, S., and E. BRUNS. 1987. Region 3. Elk survey of known winter ranges. Alberta Fish and Wildlife Files, Rocky Mountain House. 1 pp.

PAULSEN, A. C. 1975. Report on the late season elk hunt in W.M.U.'s S416 and S418 - Ya Ha Tinda. Alberta Fish and Wildlife files. Edmonton. 43pp.

SCHLEGEL, M. 1976. Factors affecting calf elk survival in north-central Idaho- a progress report. Proc. West. Assoc. State Game and Fish Comm. 56: 342-355.

SIMPSON, G. 1847. Narrative of a journey around the world in the years 1841 and 1842. H. Colburn, London. 2 vols.

SKJIONSBERG, T. 1988. Banff National Park. Eastern slopes wildlife study. 1984-1987. Banff National Park Files, Banff.

SOPER, J. D. 1970. The mammals of Jasper National Park, Alberta. Canadian Wildlife Service Report Series No. 10. 80pp.

SPRY, I. M. 1963. The Palliser expedition. MacMillan Co., Toronto. 310pp.

STELFOX, J. G. 1964. Elk in Norwest Alberta. Land-Forest-Wildlife 6(5): 14-23.

TABER, R.D., K. RAEDEKE, and D.A. McCAUGHRAN. 1982. Population characteristics. In J. W. Thomas and D. E. Toweill (Eds.), Elk of North America. Ecology and Management. Stackpole Books, Harrisburg, Pa. 698 pp.

TANNER, H. C. 1950. An investigation into the competition between elk and big-horned sheep in the Cascade valley, Banff National Park, Alberta. Unpublished report, Canadian Wildlife Service. 32pp.

THORNE, E. T., R. E. DEAN, and W. G. HEPWORTH. 1976. Nutrition in relation to successful reproduction in elk. J. Wildl. Manage. 40: 330-335.

WEBB, R. 1961. Management suggestions for the Ya Ha Tinda and "Corners" elk winter range. 1960-1961. Unpublished report. Alberta Fish and Wildlife Division Files. Edmonton. 13 pp.

APPENDIX B

DISTRIBUTION, MOVEMENTS AND MIGRATIONS

B. DISTRIBUTION, MOVEMENTS AND MIGRATIONS

This Appendix presents detailed seasonal and local distribution and movements of wapiti within the study region (Figure B.1). During the three years of field study (1977-1979), 652 observations were made, a cumulative total of 14,758 animals were counted. From 1980 to 1987, additional data were collected through various ground surveys by the author, interviews with outfitters and Government personnel, and analysis of Government Agencies reports.

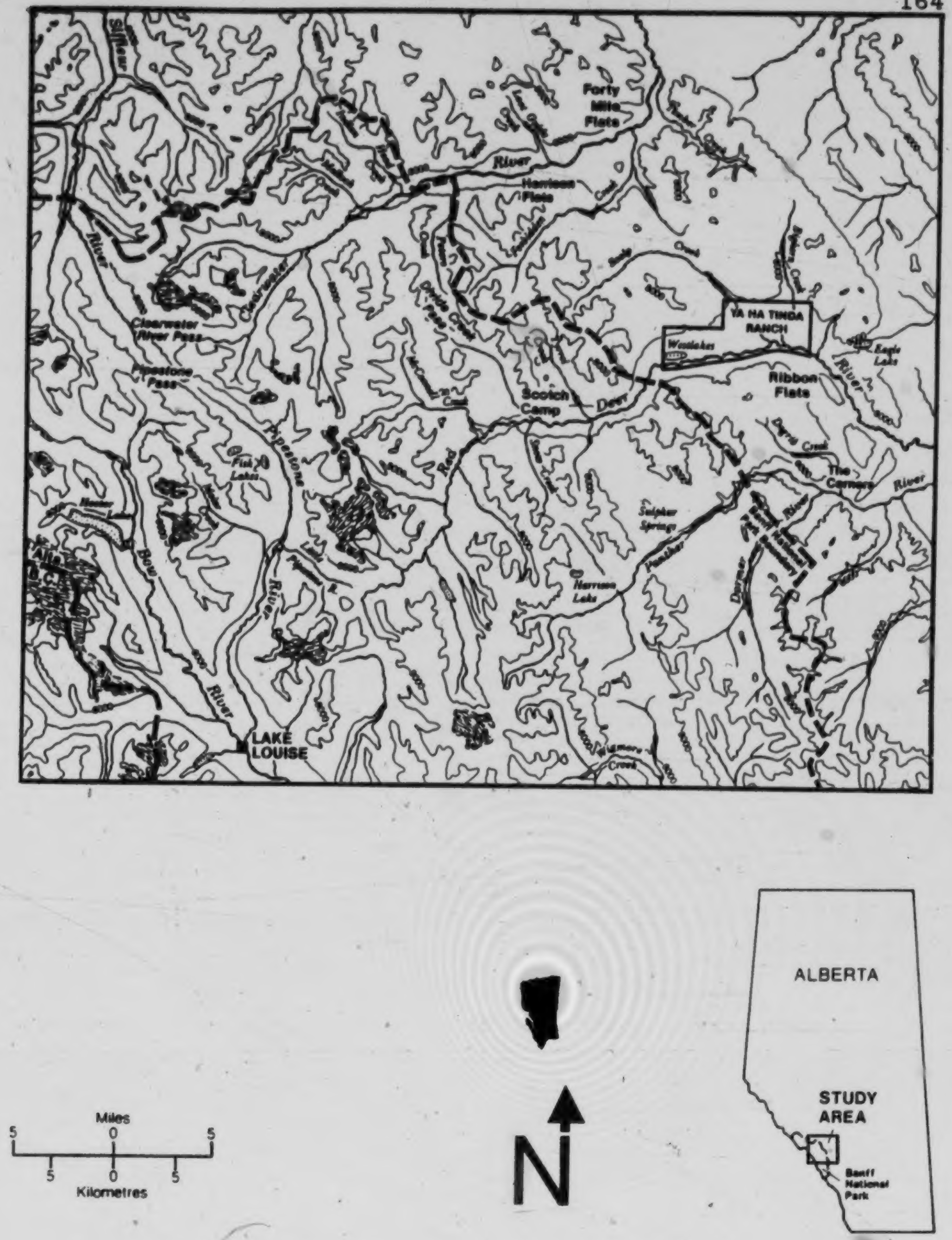
1. Distribution and movements in winter (December-April).

1.1. Red Deer River watershed.

Between 1977 and 1979, the Red Deer River watershed supported a population of about 600 animals. Wapiti that summer along the Pipestone and Little Pipestone Rivers were found to be part of the Red Deer River winter herd.

In winter, large herds of cows, calves and juveniles (50-400 individuals) were mostly found in the Ya Ha Tinda Ranch region, outside Banff National Park. In this area, during three winters, 175 observations were recorded (8,144 animals). The animals ranged from the boundary of the National Park to Eagle Lake, east of the Ya Ha Tinda Ranch. Only 25 observations (157 animals) were recorded in surrounding areas (e.g. the upper Scalp Creek, the Red Deer-Clearwater divide,

FIGURE B.1. Map of study region


Forty Mile Flats
River
Harrison Flats
Clearwater River Pass
Pipestone Pass
Pipestone
YA HA TINDA RANCH
Warden
Ribbon Flats
Scotch Camp
Red Deer
Fish Lakes
The Cornice
River
Sulphur Springs
Harrison Lake
Bow
River
LAKE LOUISE
Miles
5
0
5
5
0
5
Kilometres
N
ALBERTA
STUDY AREA
Banff National Park

Base map adapted from Dept. of Energy, Mines and Resouces, Canada.

and Ribbon Flats). The use of these areas mostly occurred during the winter hunting seasons, at other times their utilization was restricted to bulls and small herds of cows.

Few wapiti wintered in Banff National Park. During the three winters of study, wapiti were never observed west of McConnell Creek. Four observations (6 bulls) were recorded in the upper Divide Creek and seven (6 bulls and 2 cows) along Tyrrell Creek. In three instances, small herds of cows and calves (11-18 animals) were detected ranging between Scotch Camp and Tyrrell Creek meadows along the Red Deer River. In late December 1977 a herd of 30 wapiti was observed in the upper Snow Creek area.

The use of Scotch Camp and Tyrrell Creek meadows in the National Park was markedly higher (15 observations, 172 animals) in the first two weeks of January and February 1977 and 1978, during the winter hunting seasons on the Ya Ha Tinda Ranch, than in any other winter month (Morgantini and Hudson 1985). However, within a week after the hunting seasons, the same animals re-established their traditional range outside the National Park.

The winter range of wapiti on the Ya Ha Tinda Ranch comprised several areas where, in the absence of human disturbance, large herds (50-400 animals) remained for two-three days at a time. In areas in sight of roads and human activities, wapiti moved out of cover onto the open grassland at dusk and reversed their movement at dawn. In other locations (e.g. east of Bighorn Creek, Westlake, Tyrrell Creek) wapiti remained in the open throughout the day. In early winter, travel between these areas occurred between dusk and dawn. However, during March and April, in the absence of human disturbance, movements from one area to another were frequently observed in late afternoon, 2-3 hours before sunset.

Since the winter of 1980-81, movement patterns have changed. Based on ground surveys, on surveys carried out by the Alberta Fish and Wildlife Division, and on reports of Parks Canada personnel, it appears that several areas are not used to the same level that they used to be (e.g. between Bighorn Creek and the Ya Ha Tinda Ranch buildings), while others (e.g. east of Bighorn Creek) are receiving a very high grazing pressure. This change may be related to hunting pressure by native people, vehicular activity along the Bighorn Creek road or to the presence of a large wolf pack (Appendix A, Chapter 2.1).

1.2. Clearwater River watershed.

Between 1977 and 1979, the Clearwater River watershed supported a population of approximately 200 animals. In winter, a total of 47 observations (343 animals) were recorded. Most observations occurred outside Banff National

Park, between the Park boundary and Lost Guide Creek. Wapiti made extensive use of Harrison Flats and Lost Guide Creek meadows along the Clearwater River, and of the south facing slopes in the Lost Guide Creek area. Frequent movements between these ranges were observed.

In Banff National Park during three winters, observations were limited to the Clearwater Lake area (6 bulls, 2 cows), Peters Creek (2 bulls) and Mallock Creek meadows (52 cows, 8 bulls).

Occasional winter surveys by the author between 1980 and 1987, and aerial surveys by the Alberta Fish and Wildlife Division show similar distributions. In April 1983, during a separate study on winter ranges condition (Morgantini and Russell 1983), movements of approximately 40 wapiti were followed from Forty Mile Flats to Lost Guide Creek meadows. This indicates that wapiti that in winter are occasionally observed farther east along Timber Creek (approx. 3 km) are part of the same population that summers in Banff National Park.

1.3. Panther River watershed.

Within the Panther River watershed, a population of approximately 200 wapiti wintered both inside and outside Banff National Park.

Outside the National Park, the highest number of observations (29) were recorded in the Corners area. Intensive use was made of the south east slopes above the Panther River. Wapiti were also observed along the lower Dog Rib Creek. During the special hunting seasons (Jan.-Feb. 1977 and Jan.-Feb. 1978) (Appendix A, Section 2.2.1), several large herds moved from the Corners and from the Ya Ha Tinda Ranch, to the headwaters of DogRib Creek.

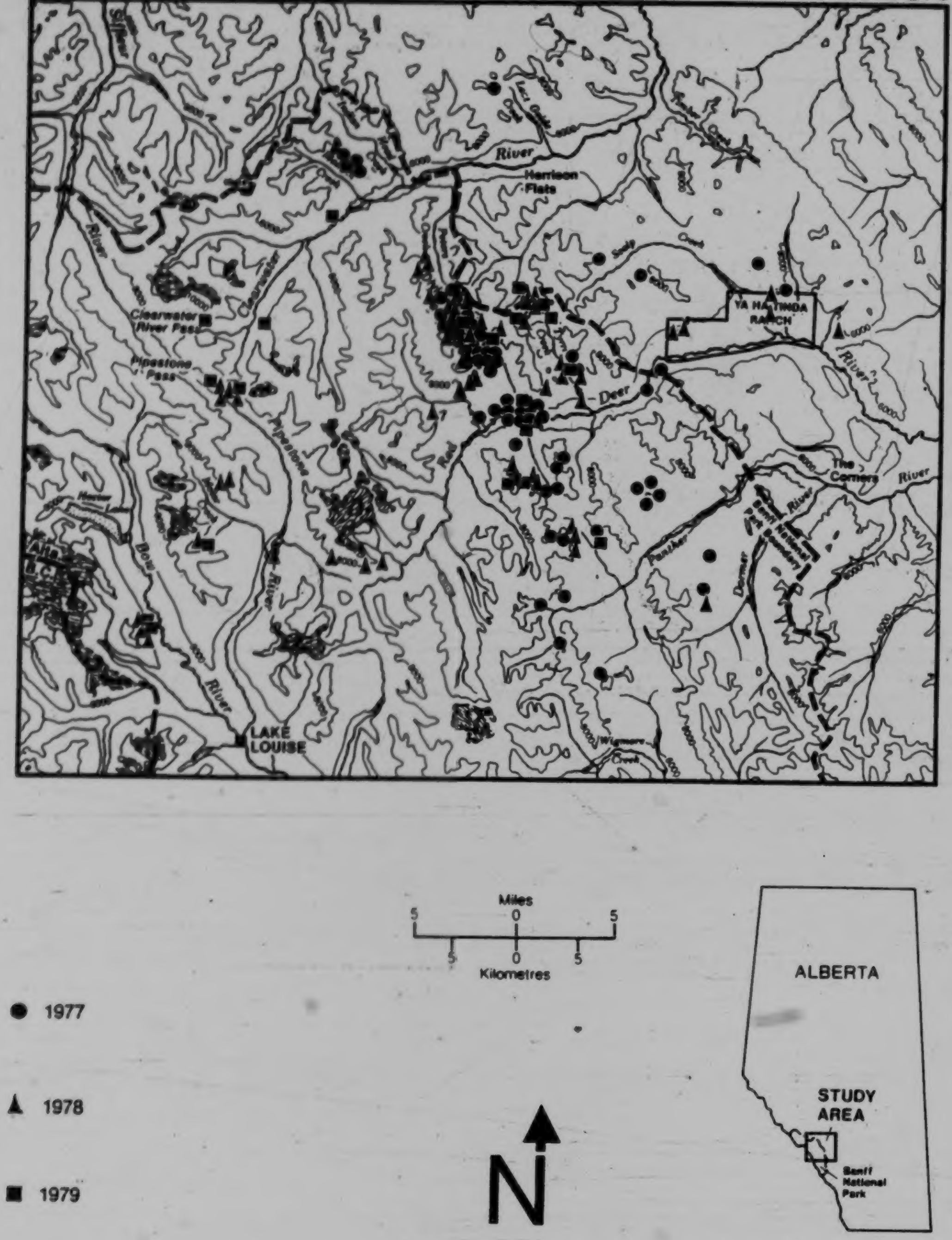
In Banff National Park, wapiti wintered along the Panther River in the Sulphur Springs area and on the surrounding meadows east and west. A large number of bulls (15 observations) and a few cows (4 observations) were found wintering on the subalpine meadows above Sulphur Springs (Panther-Red Deer divide). Bulls were also occasionally observed in the Harrison Lake area.

Winter movements across the boundary of the National Park were detected. However, it could not be determined whether they reflected normal movement patterns or whether they were caused by human disturbance in the Corners area.

2. Distribution and movements in the summer (July-August)

During the months of July and August 1977, 1978 and 1979, 118 group observations were made, for a total of 1,417 animals. The great majority were found in mountain regions within the boundary of Banff National Park, widely dispersed over some 1,600 km^2 of terrain (Figure B.2). Sixty-six

FIGURE B.2. Summer (July-August) distribution of wapiti sightings


River
Harrison Flats
Clearwater River Pass
Clearwater
Pipestone Pass
Pipestone
River
Red
Deer
YA HA TINDA RANCH
River
The Corners
River
Panther
Dormer
Banff National Park Boundary
Wigmore Creek
Bow
River
LAKE LOUISE
Alta.
B.C.
Miles
5
0
5
5
0
5
Kilometres
● 1977
▲ 1978
■ 1979
N
ALBERTA
STUDY AREA
Banff National Park

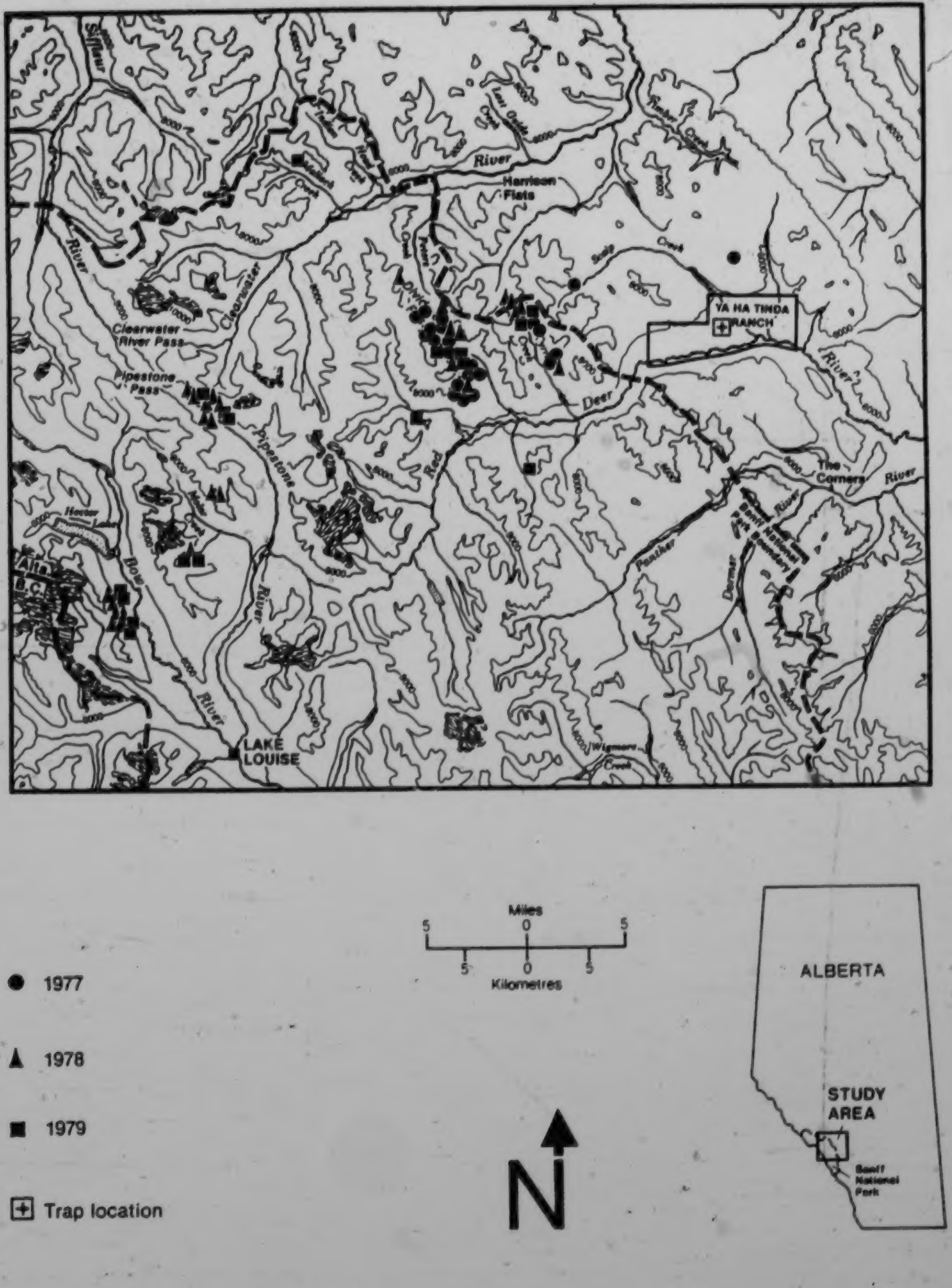
Base map adapted from Dept. of Energy, Mines and Resouces, Canada.

observations included collared animals. Their distribution reflected the wide dispersion of wapiti throughout the study region (Figure B.3).

Of a total of 23 animals collared in winter on the Ya Ha Tinda Ranch, 18 were found to summer in Banff National Park, 2 were found in the Park only in September and their summer ranges are not known, while 3 were never located and were presumed dead. In terms of river watersheds, 10 animals were found in the Pipestone-Lake Louise area, 7 in the Red Deer River watershed, 1 along the Panther River, and 2 in the Clearwater River region.

In July and August, wapiti were mostly found on high subalpine and alpine ranges at the headwaters of several creeks tributary to the Red Deer, Panther and Clearwater Rivers. The Divide Creek-Peters Creek area, the upper Tyrrell Creek and Snow Creek and their tributary valleys, Mallock creek, the Harrison Lake area, all supported resident herds (30-70 cow-calves) with well defined local movement patterns. The existence of a network of well worn trails indicates the presence in the past of significantly higher population levels. Even though these areas received the highest use, small herds of cows (1-10 animals) and bulls, and signs of their activity, were recorded throughout the National Park, wherever favorable habitat was available. Occasionally, wapiti could be observed along the river valleys (e.g. Scotch

FIGURE B.3. Summer (July-August) distribution of collared wapiti


Siffleur
River
Harrison Flats
Clearwater
Clearwater River Pass
Pipestone Pass
Pipestone
YA HA TINDA RANCH
Red
Deer
River
The Corners
River
Panther
Dormer
Banff National Park Boundary
Hector Lake
Bow
River
LAKE LOUISE
Alta.
B.C.
Wigmore Creek
● 1977
▲ 1978
■ 1979
Trap location
Miles
5
0
5
Kilometres
N
ALBERTA
STUDY AREA
Banff National Park

Base map adapted from Dept. of Energy, Mines and Resouces, Canada.

Camp) mostly while travelling to or from their summer ranges.

In 1978 and 1979, approximately 200-250 cows and juveniles that had wintered on the Ya Ha Tinda Ranch were found to summer in the Pipestone-Lake Louise area. Two radio collared wapiti from this herd and some 50 other animals were located north of Lake Louise along the Bow River valley, while three other radio collared animals (with approximately 150-200 others) ranged throughout the summer along the Pipestone River, from Molar Creek and its tributary valleys to the upper Pipestone River and Fish Lakes area.

As previously indicated, more than 90% of the total winter population of the region spent the summer inside Banff National Park. However, approximately 70 animals, mostly small herds of cows and calves and isolated bulls, were found to reside throughout the summer outside the Park boundary. The highest number (30 individuals) was observed in the Clearwater watershed in the upper Lost Guide Creek valley. One herd of 5-15 animals ranged on the Ya Ha Tinda Ranch and was frequently observed by Parks Canada personnel in the aspen-pine forests behind the Ranch buildings (S. Haugen pers. comm.). Isolated bulls were observed along Bighorn Creek, DogRib Creek and on the subalpine and alpine ranges above Ribbon Flats. Wapiti signs were occasionally recorded in the upper DogRib Creek and in the small valleys along the Red Deer River south of the Ya Ha Tinda Ranch.

In the summer of 1977, a herd of 34 animals (three spike bull~~s, two~~ young bulls, 21 cows and 8 calves) with two collared individuals (cow #9 and #15) remained on the Ya Ha Tinda Ranch until the third week of July. When disturbed by hikers and trail riders, the animals moved onto the alpine meadows between Bighorn Creek and Scalp Creek, where they resided until the first week of August. After continuing harassment by 4X4 vehicles, the animals left the region. In spite of extensive surveys, this herd was not located until September 28, when the two collared animals were found in the Tyrrel Creek area in Banff National Park, indicating a late summer migration of 30 kilometers. One other herd (at least 85 individuals) resided in the upper Scalp Creek on the high plateau overlooking Forbidden Creek until the first week of August. By the middle of August, in spite of extensive surveys, the herd could not be located. It is believed to have dispersed in the heavy timber on the Forbidden Creek side and moved into Banff National Park. This is supported by circumstantial evidence, such as signs and tracks along existing trails, absence of wapiti activity in the Forbidden Creek area and a higher number of animals in the upper Tyrrell Creek than observed in July. This range abandonment is thought to be related to the disturbance associated with the drilling of a gas well in the upper Scalp Creek.

In the summer of 1983, during aerial surveys carried out by the Alberta Fish and Wildlife Division outside Banff National Park (Nette 1983), 112 and 87 wapiti were observed on sub-alpine and alpine meadows within the Red Deer River and the Clearwater River watersheds. The surveys are overall consistent with the results of this study and indicate that only a small percentage of the animals that winter along the Red Deer River summers outside Banff National Park. The apparent higher number of animals observed reflects higher population levels. However they may also indicate the re-establishment of traditional summer ranges.

3. Spring and fall migrations

Throughout the study region, the majority of the wapiti population exibited well-defined seasonal migrations between winter and summer ranges. The travel distance to National Park summer ranges averaged 50 kilometers (Table B.1).

Wapiti showed a strong tendency to return to the same summer ranges every year. However, there were instances where animals were observed in successive years on different summer ranges. For instance, elk #16 was located in the Divide Creek area in 1977 and in the upper Pipestone River in 1978 and 1979. The two ranges are some 40 km apart. In 1978 elk #5 summered in the Peters Creek area, but in the summer of 1979 it ranged in the upper Mallock Creek. Late summer movements between different ranges by elk #9 and #15 have been

Table B.1. Location of summer ranges in Banff National Park and distances from the Ya ha Tinda Ranch winter range (1977-1979).

Animal No.	Location of summer ranges	Linear distance (km)	Actual minimum travel distance (km)*
1	Upper Pipestone River	47.5	67.5
2	Upper Pipestone River	47.5	67.5
3	North Lake Louise	57.5	67.5
4	South Molar Creek	51.0	62.5
5	Peters Creek (1st sum.)	28.0	37.0
"	Mallock Creek (2nd sum.)	37.0	47.0
6	Upper Tyrrel Creek	17.5	26.5
7	Upper Divide Creek	25.0	30.0
8	North Lake Louise	57.5	67.5
9	Upper Tyrrel Creek	17.5	26.5
10	Upper Pipestone River	47.5	67.5
11	Upper Divide Creek	25.0	30.0
12	Upper Tyrrel Creek	17.5	26.5
13	Upper Molar Creek	47.5	62.5
14	" " "	47.5	62.5
15	" " "	47.5	62.5
16	Up. Divide Cr. (1st sum.)	25.0	30.0
"	Up. Pipestone (2nd sum.)	47.5	67.5
"	" " (3rd sum.)	47.5	67.5
17	Upper Tyrrel Creek	17.5	26.5
18	Panther-Red Deer summit	35.0	43.0

* Minimum travel distance along river valleys.

previously described.

Along the migratory routes, wapiti used the following intermediate ranges: the meadows between McConnell and Tyrrel Creeks in the Red Deer River watershed, Mallock Creek meadows along the Clearwater River, and Sulphur Spring meadows and sidehills along the Panther River.

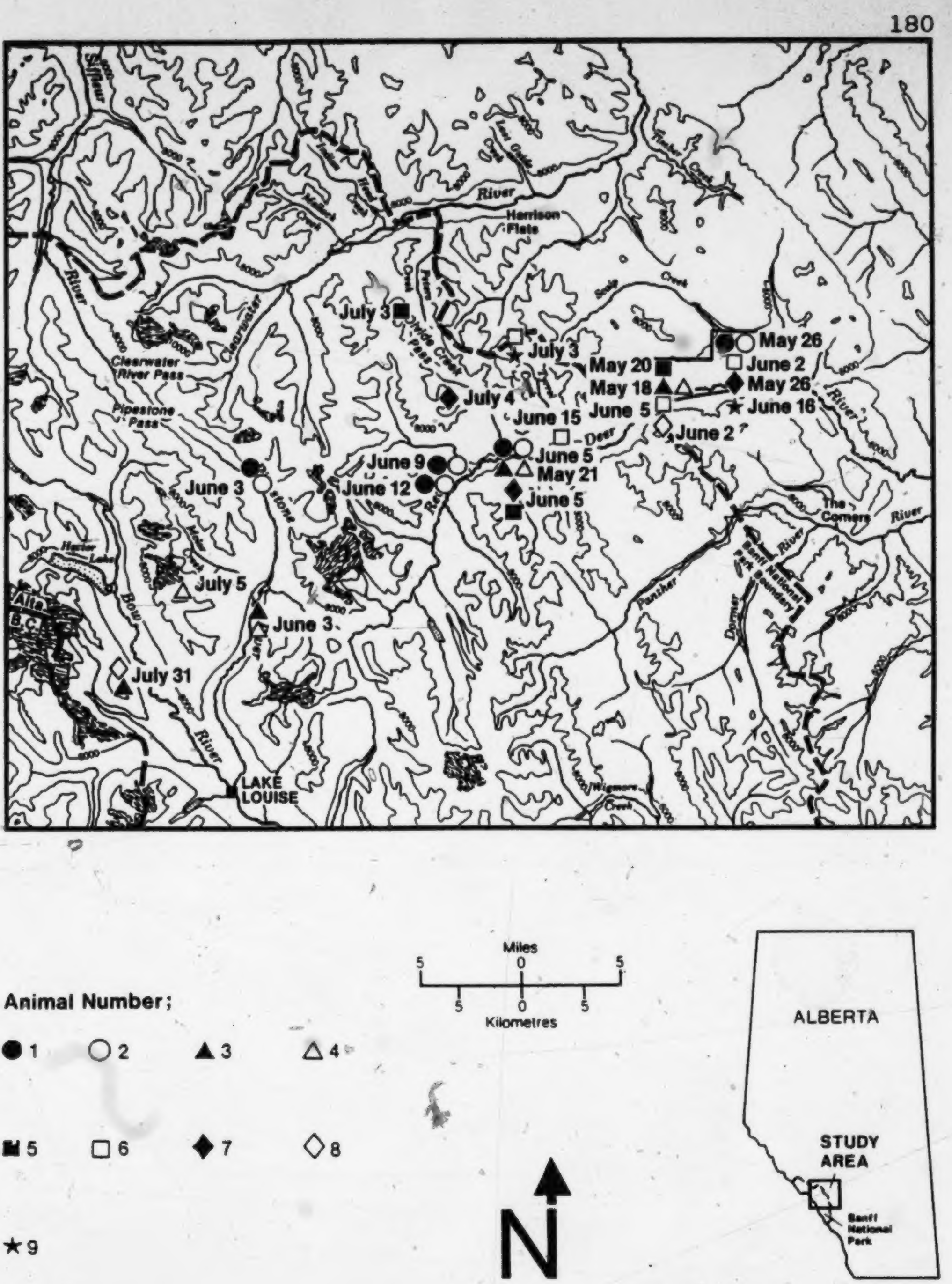
The overall migratory pattern, as described in Chapter 3, was documented through intensive field surveys and is further seen in the travel pattern of radio-collared animals (Figures B.4 and B.5).

4. Herd boundaries

The elk population in the region can be subdivided into three separate herds each associated with a major river valley (i.e. Panther, Red Deer and Clearwater Rivers). Some mingling between herds on summer ranges was detected in the Divide Creek (Red Deer-Clearwater herds) and Snow Creek (Panther-Red Deer herds) areas. However, in early fall the great majority of the animals that had shifted to another drainage (e.g. Peters Creek in the Clearwater drainage) were observed to move back to their habitual ranges. Further mingling may occur in late fall and winter, especially during intensive human harassment, between the Panther and Red Deer herds within the Corners-Dog Rib-Ribbon Flats area.

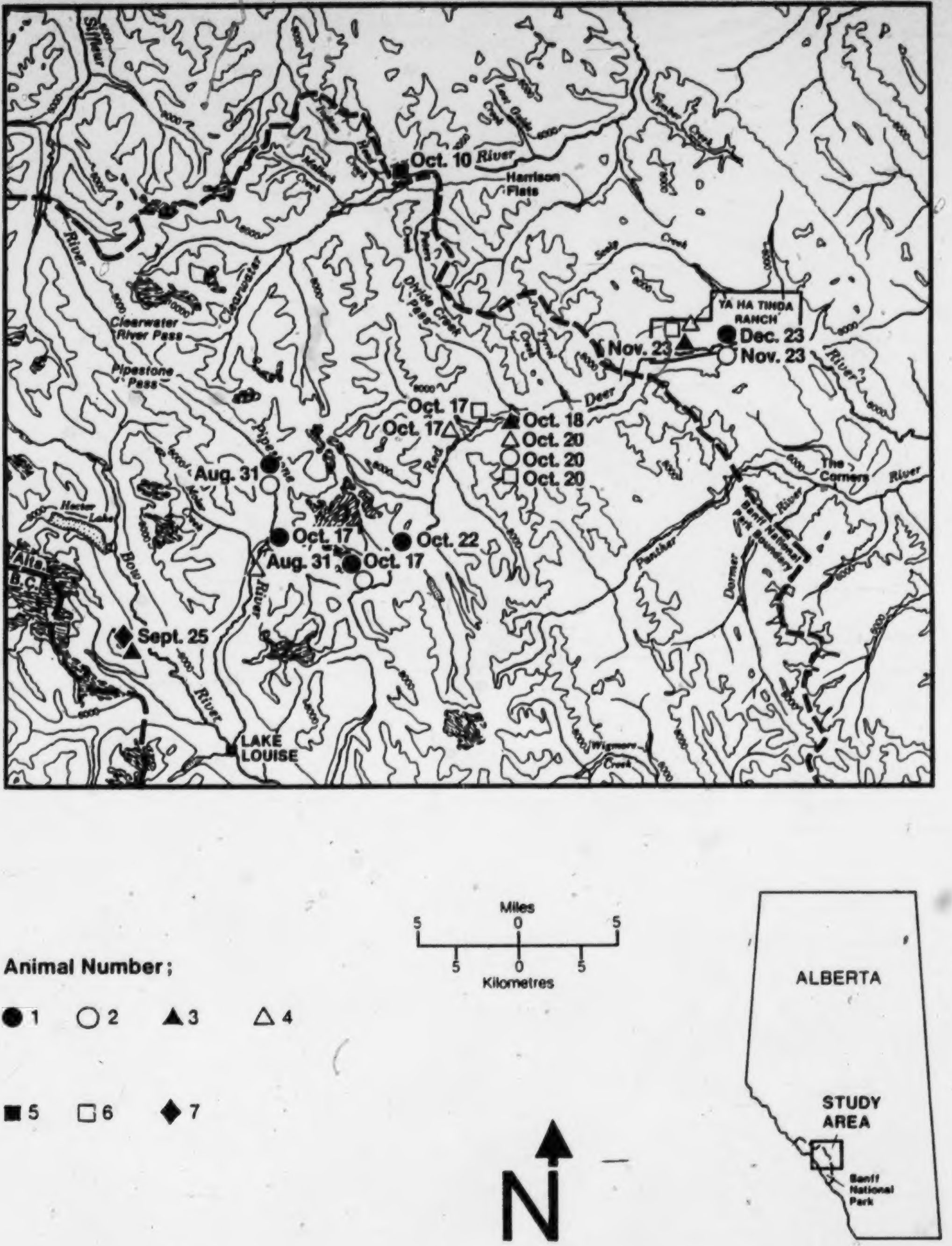
Movements of elk from and to areas adjacent to the study

FIGURE B.4. Late spring movements of 9 collared wapiti from winter to summer ranges (1978).


July 3
July 3
May 26
June 2
May 20
May 18
May 26
June 5
June 16
June 2
July 4
June 15
June 5
May 21
June 9
June 12
June 3
June 5
July 5
June 3
July 31
Harrison Flats
Clearwater River Pass
Pipestone Pass
Clearwater
Deer
River
The Corners
Panther
Dormer
Banff National Park Boundary
Bow
River
Hector Lake
Alta.
B.C.
LAKE LOUISE
Wigmore Creek
Animal Number;
● 1
○ 2
▲ 3
△ 4
■ 5
□ 6
◆ 7
◇ 8
★ 9
Miles
5
0
5
5
0
5
Kilometres
N
ALBERTA
STUDY AREA
Banff National Park

Base map adapted from Dept. of Energy, Mines and Resouces, Canada.

FIGURE B.5. Fall movements of 7 collared wapiti from summer to winter ranges


Oct. 10
River
Harrison Flats
Siffleur
River
Clearwater
Clearwater River Pass
Pipestone Pass
Pipestone
Divide Creek Pass
Red Deer
Ya Ha Tinda Ranch
Nov. 23
Dec. 23
Nov. 23
Oct. 17
Oct. 17
Oct. 18
Oct. 20
Oct. 20
Oct. 20
Aug. 31
Oct. 17
Oct. 22
Aug. 31
Oct. 17
Hector Lake
Bow
River
Sept. 25
Alta.
B.C.
Lake Louise
Panther
Dormer
River
Banff National Park Boundary
The Corners
Wigmore Creek
Animal Number;
● 1
○ 2
▲ 3
△ 4
■ 5
□ 6
◆ 7
Miles
5
0
5
5
0
5
Kilometres
N
ALBERTA
STUDY AREA
Banff National Park

Base map adapted from Dept. of Energy, Mines and Resouces, Canada.

region were observed. While no evidence was ever found of movements from the Red Deer herd across Pipestone Pass into the Sifleur River, travel through Clearwater Pass into the Sifleur River valley was detected. Mingling may also occur between the Red Deer River and the Bow River herds as indicated in 1977 by the presence (in the Molar Creek area and on the Ya Ha Tinda Ranch) of one elk that had been collared in Kootenay National Park (in the Molar Creek area and on the Ya Ha Tinda Ranch). Wapiti from Kootenay National Park have been reported to summer along the Bow River (Gibson and Baker 1977). In 1978, two elk not collared during this study were found within the Red Deer River herd. They had been trapped in Jasper National Park and released by the Alberta Fish and Wildlife Division in 1974 along the Red Deer River, east of the Front Ranges, 25 km from the Ya ha Tinda Ranch.

Mingling between the Clearwater River herd and the elk population along Ranger Creek and Ram River, across the upper Indian Head and Lost Guide Creek, were not monitored.

With regard to the Panther River herd, there is historical evidence of movements of animals from this herd to the Dormer River and the upper Wigmore Creek-Cascade River area (Banff National Park files).

5. Literature cited

GIBSON, T., and K. BAKER. 1976. Elk study Kootenay National

Park. Interin Report. Indian and Northern Affairs. Parks Canada, Calgary. 45 pp.

MORGANTINI, L. E., and R. J. HUDSON. 1985. Changes in Diets of Wapiti during a Hunting season. J. Range Manage 38: 77-79.

MORGANTINI, L. E., and W. B. RUSSELL. 1983. An assessment of three selected elk winter ranges in the Rocky Mountains region. Unpubl. rep. prepared for the Alberta fish and Wildlife Division by Wildlife Resources Consulting Ltd. Alberta Fish and Wildlife Files, Edmonton. 265 pp.

NETTE, T. 1983. Elk surveys (Summer 1983) of the Rocky Mountain House Area. Alberta Fish and Wildlife Files, Rocky Mountain House. 36 pp.

APPENDIX C

Table C.1. Average size of cow-calf-yearling
herds as determined by habitat.
Winter.

ANOVA

Source of variation	SS	df	MS	F-ratio	Sig. level
Between groups	107551.43	9	11950.15	2.616	0.0076
Within groups	721666.52	158	4567.51		
Total (corr.)	829217.95	167			

Table of average herd sizes per habitat (Winter)

Habitat	n	Average	St. Err.
Alpine tundra	4	41.5abcdef	13.37
Avalanche slopes	1	30.0abcd	0.00
High el. open forests	4	13.2a	1.10
Grassland slopes	17	17.7ab	2.53
Spruce forests	17	38.7abcde	15.11
Pine forests	16	51.4a cdef	19.24
Low el. shrublands	21	96.5 d g	17.40
Low el. grasslands	63	75.4 cd fg	10.15
Deciduous forests	3	26.7abc	24.18
Riverine habitats	22	36.8abcde	8.45

Values followed by the same letters are part of homogeneous groups ($P<0.05$; multiple range test).

Table C.2. Average size of cow-calf-yearling herds as determined by habitat. Spring

ANOVA

Source of variation	SS	df	MS	F-ratio	Sig. level
Between groups	7092.12	9	788.01	1.309	0.2362
Within groups	93298.82	155	601.92		
Total (corr.)	100380.95	164			

Table of average herd sizes per habitat (Spring)

Habitat	n	Average	St. Err.
High el. shrubland	3	5.6abc	1.85
Avalanche slopes	1	1.0a	0.00
High el. open forests	1	1.0a	0.00
Grassland slopes	12	4.1ab	0.91
Spruce forests	16	19.7a c ef	8.07
Pine forests	19	20.8a c f	5.30
Low el. shrublands	22	21.4a c f	6.92
Low el. grasslands	67	20.7a c f	3.14
Deciduous forests	12	6.6abcd	2.64
Riverine habitats	12	7.3abcde	2.80

Values followed by the same letters are part of homogeneous groups (P<0.05; multiple range test).

Table C.3. Average size of cow-calf-yearling herds as determined by habitat. Summer.

ANOVA

Source of variation	SS	df	MS	F-ratio	Sig. level
Between groups	6442.62	10	644.26	2.094	0.0337
Within groups	25847.31	84	307.70		
Total (corr.)	32289.94	94			

Table of average herd sizes per habitat (Summer)

Habitat	n	Average	St. Err.
Alpine tundra	18	26.8 b	5.55
Krummholz	12	8.0a	2.77
Upper el. shrubl.	1	16.0ab	0.00
Avalanche slopes	23	22.6 b	4.91
High el. open forests	4	16.0ab	7.33
Grassland slopes	3	3.3a	1.85
Spruce forests	4	17.0ab	5.14
Pine forests	5	5.0a	2.50
Low el. shrublands	6	8.6a	2.29
Low el. grasslands	15	9.4a	2.92
Deciduous forests	4	5.0a	2.48

Values followed by the same letters are part of homogeneous groups ($P<0.05$; multiple range test).

Table C.4. Average size of cow-calf-yearling herds as determined by habitat. Fall.

ANOVA

Source of variation	SS	df	MS	F-ratio	Sig. level
Between groups	752.26	8	94.03	.638	0.7417
Within groups	7218.51	49	147.31		
Total (corr.)	7970.77	57			

Table of average herd sizes per habitat (Fall)

Habitat	n	Average	St. Err.
Alpine tundra	4	7.2a	6.06
Upper el. shrubl.	1	16.0abc	0.00
Avalanche slopes	3	8.0a	1.52
Grassland slopes	14	16.9abc	5.49
Spruce forests	2	5.5a	2.50
Pine forests	11	8.6ab	1.96
Low el. shrublands	1	5.0a	0.00
Low el. grasslands	19	10.8abc	1.61
Deciduous forests	3	11.0a c	7.09

Values followed by the same letters are part of homogeneous groups ($P<0.05$; multiple range test).

Table C.5. Average size of bull herds as determined by habitat. Winter.

ANOVA

Source of variation	SS	df	MS	F-ratio	Sig. level
Between groups	5.68	7	.81	.681	0.6867
Within groups	32.20	27	1.19		
Total (corr.)	37.88	34			

Table of average herd sizes per habitat (Winter)

Habitat	n	Average	St. Err.
Avalanche slopes	5	2.0ab	0.54
High el. open forests	2	2.5 b	1.50
Grassland slopes	5	2.0ab	0.55
Spruce forests	5	2.0ab	0.32
Pine forests	3	1.0a	0.00
Low el. shrublands	8	2.0ab	0.38
Low el. grasslands	5	2.6 b	0.51
Riverine habitats	2	2.5 b	0.50

Values followed by the same letters are part of homogeneous groups ($P<0.05$; multiple range test).

Table C.6. Average size of bull herds as determined by habitat. Spring.

ANOVA

Source of variation	SS	df	MS	F-ratio	Sig. level
Between groups	21.08	4	5.27	1.144	0.3860
Within groups	50.67	11	4.61		
Total (corr.)	71.75	15			

Table of average herd sizes per habitat (Spring)

Habitat	n	Average	St. Err.
Grassland slopes	1	6.0 b	0.00
Spruce forests	2	2.0ab	0.00
Low el. shrublands	3	1.7a	0.33
Low el. grasslands	9	3.3ab	0.83
Deciduous forests	1	1.0a	0.00

Values followed by the same letters are part of homogeneous groups (P<0.05; multiple range test).

Table C.7. Average size of bull herds
as determined by habitat.
Summer.

ANOVA

Source of variation	SS	df	MS	F-ratio	Sig. level
Between groups	752.26	8	94.03	.638	0.7417
Within groups	7218.51	49	147.31		
Total (corr.)	7970.77	57			

Table of average herd sizes per habitat (Fall)

Habitat	n	Average	St. Err.
Alpine tundra	8	3.5a	1.34
Krummotz	3	2.3a	1.33
Avalanche slopes	1	1.0a	0.00
High el. open forests	5	1.2a	0.20
Grassland slopes	1	1.0a	0.00
Spruce forests	1	1.0a	0.00
Low el. shrublands	2	2.5a	0.50
Low el. grasslands	2	2.0a	1.00

Values followed by the same letters are part
of homogeneous groups ($P<0.05$; multiple range test).

Table C.8. Average size of bull herds
as determined by habitat.
Fall.

ANOVA

Source of variation	SS	df	MS	F-ratio	Sig. level
Between groups	752.26	8	94.03	.638	0.7417
Within groups	7218.51	49	147.31		
Total (corr.)	7970.77	57			

Table of average herd sizes per habitat (Fall)

Habitat	n	Average	St. Err.
Grassland slopes	2	1.0a	0.00
Spruce forests	2	1.0a	0.00
Pine forests	11	1.1a	0.09
Low el. shrublands	1	1.0a	0.00
Low el. grasslands	17	1.1a	0.08
Deciduous forests	3	1.0a	0.00

Values followed by the same letters are part
of homogeneous groups (P<0.05; multiple range test).